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Studies on the
PACIFIC PILCHARD or
SARDINE (*Sardinops Caeulea*)

SPECIAL SCIENTIFIC REPORT: FISHERIES No. 15

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

Explanatory Note

The series embodies results of investigations, usually of restricted scope, intended to aid or direct management or utilization practices and as guides for administrative or legislative action. It is issued in limited quantities for the official use of Federal, State or cooperating agencies and in processed form for economy and to avoid delay in publication.

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United States Department of the Interior
Oscar L. Chapman, Secretary
Fish and Wildlife Service
Albert M. Day, Director

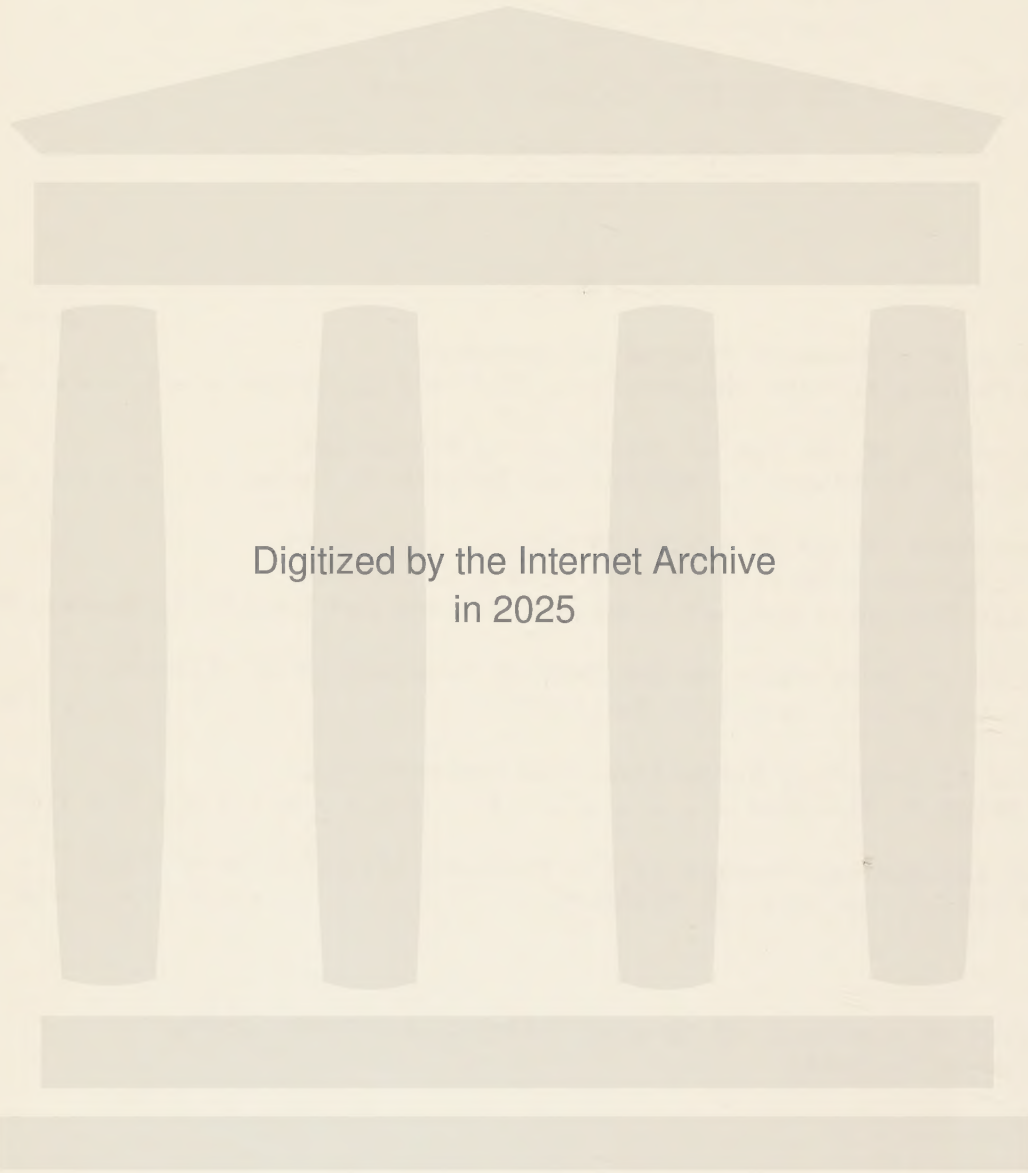
Special Scientific Report - Fisheries
No. 15

STUDIES ON THE PACIFIC PILCHARD OR SARDINE
(SARDINOPS CAERULEA)

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1. Structure of a Research Program to Determine How Fishing Affects
the Resources

By

Oscar E. Sette 1/

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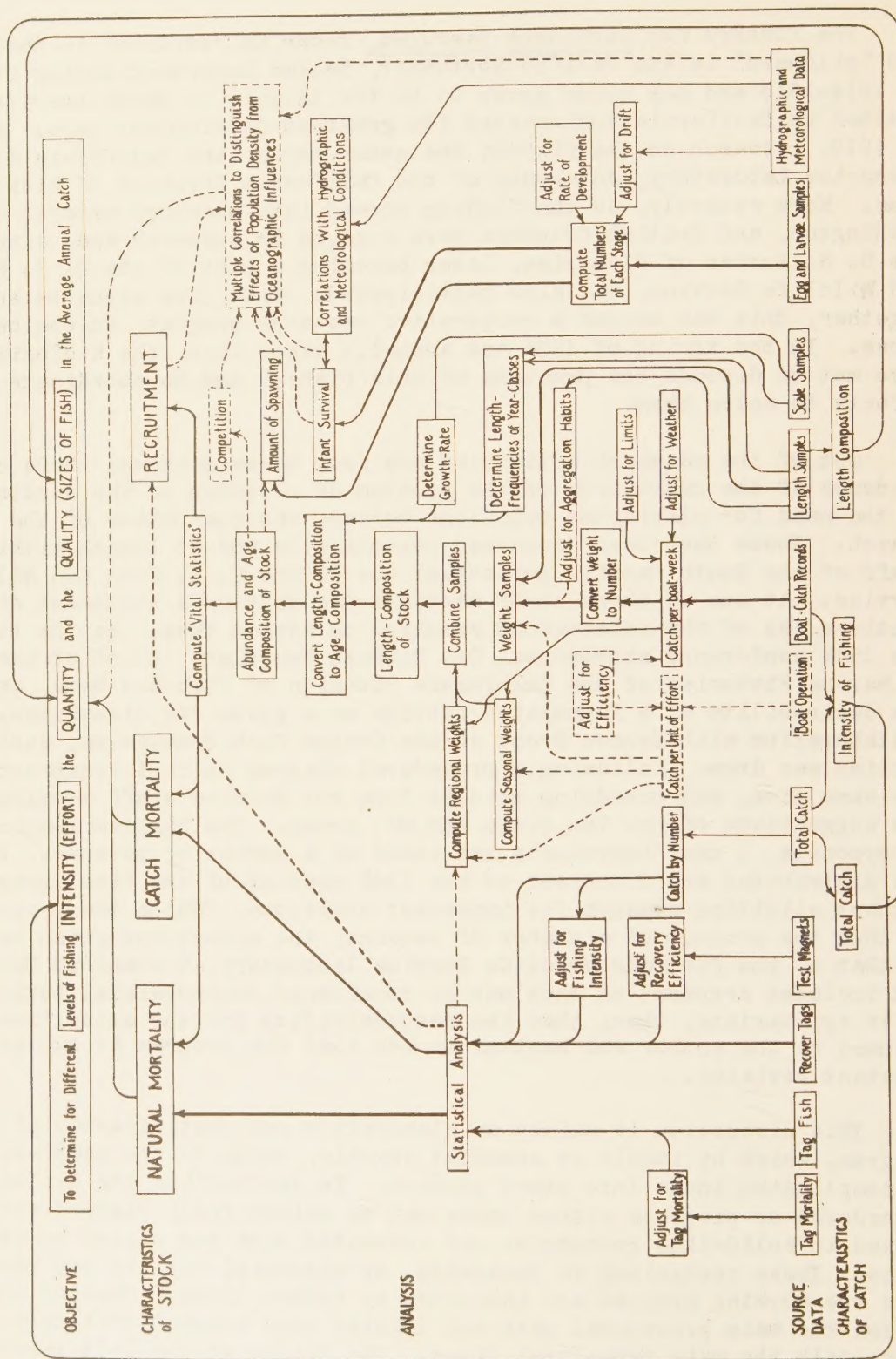
INTRODUCTION

The fishery for Sardinops caerulea, known as "sardine" in California and "pilchard" in the Pacific Northwest, became important during the war of 1914-1918 and has since grown to be the largest in North America. It started in California and reached its greatest development here. As early as 1919, research on the fishery was under way by the California State Fisheries Laboratory, an agency of the California Division of Fish and Game. More recently, as the fishing spread into northern waters, Oregon, Washington, and British Columbia have engaged in research and, since 1937, the U. S. Bureau of Fisheries, later becoming a part of the U. S. Fish and Wildlife Service, has also participated. With five agencies working together, this has become a cooperative research program, in the best sense. In the spring of 1936 and annually since then, the biologists have met to discuss the problems of this fishery and to coordinate their efforts to solve them.

Out of the research activities and from these meetings there came evidence of the complexity of the problem of research on the sardine and of the need for clarifying relations between various phases of the research. These have been discussed periodically and at length within the staff of the South Pacific Investigations of the U. S. Fish and Wildlife Service. At one of these staff meetings was drafted a statement of objectives and of the information required to attain them. As the time for the 1942 conference approached, Dr. Richard Van Cleve, Chief of the Bureau of Marine Fisheries of the California Division of Fish and Game, suggested the desirability of a formulated outline as a guide for discussion. In collaboration with Vernon Brock of the Oregon Fish Commission, such an outline was drawn, following a procedural diagram which I constructed at the same time, and embodying results from our Service staff meetings and the suggestions of Dr. Van Cleve and Mr. Brock. The diagram mentioned (opposite) thus represents the ideas of a number of persons. It was distributed and discussed at the 1942 meeting of the five agencies without eliciting demands for important revisions. While the program is thus the product of a number of persons, the exposition given herewith is that of the Fish and Wildlife Service laboratory at Stanford University and includes argument on what may be considered controversial topics. It is appropriate, then, that the responsibility for the exposition be assumed by the author who hastens to add that the program is subject to constant revision.

This discussion is mainly an elaboration and justification of the diagram, which by itself is somewhat cryptic, owing to the compression of complicated ideas into short phrases. In the outline the titles of procedures or projects either under way or rather fully planned are enclosed in solid-line rectangles and connected with the others by solid lines. Those recognized as desirable or essential but not yet integrated into the working program are indicated by broken lines. Heavier lines follow the main procedural path and lighter ones connect tributary adjustments with the main procedural lines. The titles at the left margin,

STRUCTURE OF A PROGRAM FOR PACIFIC SARDINE RESEARCH



not enclosed by rectangles, refer to material to the right of each. To preserve the closest possible connection between text and diagram, the exact phraseology used in the diagram is repeated as headings in the text, even though, in some instances, it results in rather awkward context.

Objective

Underlying the investigations of the U. S. Fish and Wildlife Service on the Pacific sardine or pilchard are certain ideas or theories, the discussion of which will clarify that of objectives. In the first place, it is recognized that before fishing took place the sardine population had filled its ecological niche and that, apart from fluctuations such as occur among all organisms, the deaths, on the average, equaled the births and the population was in equilibrium, i.e. neither increasing nor decreasing in total numbers. Moreover, the deaths under these conditions were all due to "natural" causes. Predators were, of course, responsible for a substantial portion of the natural mortality; but the basic influence tending to keep the population in check must have been competition within the population. This competition may have been of many different forms, all, however, connected with the density of the population itself. It might be failure in reproduction which could arise from the overabundance of spawners, the debilitating effects of which might affect the viability of their eggs; or if the viability of eggs were unaffected, simple spread into marginal spawning grounds with consequent failure of eggs to hatch would keep the population in check. Or the competition might simply increase mortality through division of a limited food supply among more mouths. Or the pilchard population, grown to maximal size, might so well supply predators with food that they would multiply to an extent which would check further increase of the pilchards. Whatever the mechanism, the existence of a depressing effect of population size on population increase is implicit in the idea of natural population equilibrium. It also involves negation of the idea that a fishery can ultimately destroy a population.

What, then, happens when an important amount of fishing takes place? There is an added cause for deaths. These deaths are largely among adults, and to the extent that catch mortality goes beyond replacing natural mortality, that is, to the extent that fishermen take fish that would not be eliminated by sharks and other predators, the number of adults in the population is reduced and the size composition is changed in the direction of fewer large individuals. But the fact that the population grows lesser in numbers and its individuals smaller in size, is no proof that the fishery is taking more than it ought to take, for another thing is happening at the same time. The depressing effect of population-size on population-increase is diminishing. If internal competition had been strongest among the commercial sizes, catch mortality would largely replace natural mortality and the population decrease would be slight. If it had been strongest among pre-commercial sizes or between commercial sizes on the one hand and pre-commercial sizes on the other hand, then replenishment of the commercial population would increase somewhat in proportion to the amount of "thinning out."

So far the argument has been speculative. But it is not necessary to rest on this. There have been many experiments in which populations have been reared under laboratory conditions. These have involved such diverse forms as yeast, diatoms, protozoans, insects, and even fishes. In all of them the rate of increase was rapid while the population was small and slowed down as it grew larger, finally reaching a size beyond which there was no increase. Initially, when the population is small, even though the reproductive rate is high, relatively few individuals are added because there are only a few producers. Finally, when the population is at its maximum and there are many reproducers, there are also relatively few individuals added, either because the reproductive rate has become depressed or because mortality has become so high as to offset the additions from reproduction. Usually both a depressed birth rate and increased mortality operate together to keep the net increase in numbers of individuals at a minimum. In contrast to the small increase in population-size at both low and high population densities, is the large increase that takes place when the population is about midway between these extremes. Then, the population is large enough to have many reproducers and small enough so that the reproductive rate has not been greatly lowered and mortality has not yet been intensified. In this state, the increase in numbers of individuals per unit of time is large.

The lesson is obvious. A population has its maximum increase when it is neither at maximum, nor minimum, size, but when middling in size; and that is the level at which the most individuals can be regularly removed and still be fully replenished by the population's inherent tendency to grow.

Of course, with a population of fishes in their natural habitat, things are not as simple as in these experiments. With the pilchard it is almost beyond question that predation would be a large influence. Fortunately, there have been population experiments that included the element of predation. In these it has been shown that the predator population increases as the prey increases - with a time lag, to be sure. Therefore, holding a prey population at a middling size would similarly limit its predators, especially with a species like the pilchard which is in a dominant position among prey fishes. So the factor of predation should not greatly alter the fact that replacement will be maximal in a medium-size population. The time lag in the growth curves of composite predator-prey populations does introduce fluctuations and may disturb not only the general level but also the precise level at which the prey-population would otherwise have its maximal replacement. This, however, does not affect the general concept.

According to this idea, the optimal amount of fishing would be that which lowers the population numbers to a level at which maximum increase takes place. Such a fishery will remove only as many fish as will be replaced and the number removed will be the largest number that can be regularly removed without further disturbing the population-size.

However, there are things to be desired in a commercial fishery beyond merely a continuing yield of maximal numbers of fish. The stock must be sufficiently abundant to be economically fishable and the sizes of fish in the catch should be economically desirable.

At the present stage of research on the pilchard population, we do not have any notion of the level at which maximum replacement would take place, nor as to whether the abundance at that level would be an economic one or whether the size composition would be commercially desirable. We can, however, be confident that the replacement, the abundance, and the size composition will be affected by the fishing intensity; and we can be sure also that we shall want the replacement to be equal to the catch so that no continuous decrement will ensue.

Therefore, for the time being, the objective is "to determine at various levels of fishing intensity the quantity and quality (sizes of fish) in the average annual catch." Choice of the optimum intensity can then be made among the consequences of the various fishing intensities according to what is economically and socially desirable. That will undoubtedly involve other than biological considerations.

It should be noted particularly that it is not an objective to determine whether abundance is decreasing. The population can be expected to decrease long before maximal yield is reached. It is not along an objective to determine whether the average size of the fish is decreasing. This probably will be the finding but is not of itself a sufficient indicator of a desirable or undesirable situation. No mention is made of protection of spawners or of spawning grounds, or of size limits, or of closed seasons, or of wasteful practices in utilization, or of other topics that often are the concern of conservationists. These items may or may not be involved eventually. At this time, they are secondary to the determination of what consequences attend different amounts of fishing and cannot be intelligently considered until these are known. In fact, the method of conserving a commercial fishery involves social, economic, and political considerations and lies in the field of political economy. Biologists need only determine the consequences of certain actions and make them known to the law-makers and administrators.

Characteristics of Catch and Stock

The objectives are stated in terms of what will be caught at different levels of fishing intensity. With sufficient information, the characteristics of the catch could be defined each season, and over a long time, empirical curves could be made that would show the relationship of intensity of fishing with quantity and quality of catch. Indeed, save for data on fishing intensity, ready collection of which was precluded by certain practices of the fishery, this job of biological accounting has been done by the California State Fisheries Laboratory over a period of 23 years during which the fishing intensity has varied widely.

Had it been possible, to include fishing intensity or its complement, relative abundance^{1/}, today's task would be enormously facilitated. Even so, it would be necessary to relate or transform the characteristics of catch to those of the stock, for replenishment depends on the fish that are left in the sea.

Of course, if the fishery took a random sample of what is in the sea, the characteristics of catch would be the same as those of stock. But if we can be sure of only one thing, it is that the fishery does not take a random sample. In the Pacific Northwest (Oregon, Washington, and British Columbia) the fishery over-samples the older fish; in southern California, the young. In Central California, it perhaps over-samples those of intermediate ages. In certain areas between ports, notably off northern California and southern Oregon, there is no fishing. At a single port, the size composition changes significantly from day to day, week to week, and month to month, and there is no assurance that the catch of the various sizes is proportional to their relative abundance in the sea. In fact, it is obvious that the various components of the stock are represented in the catch in proportion to the length of time each is subject to fishing in a particular area and not at all in proportion to its abundance in the sea.

Thus the major problem of research is how to deduce the characteristics of the stock from the available samples in the catch. Once those are known, total mortality can be estimated by computational processes developed by Baranov, Thompson and Bell, Ricker, and others. Also under certain conditions, it will be possible to separate natural from catch mortality; and both being known, to compute the recruitment (the equivalent of the actuary's birth-rate, taken as of the attainment of commercial size).

Analysis

In the diagram, the central part-analysis is taken up with the processes concerned with adjustments, conversions, and combinations intended to transform data from the catch into attributes of the stock. These processes leading to "vital statistics" are so complex that simple appraisals of their reliability by conventional statistical methods are unavailing. Confirmation must, therefore, be sought in results attained through independent approaches. The only other approach that is currently being followed is tagging. The processes involved in this branch of research are noted in the left-hand portion of the diagram and will be discussed under the heading of "Tagging research." Even after determinations of mortality and recruitment have been made by two methods and one found to verify the other, it is still necessary to investigate recruitment because changes in it are of differing significance, depending on whether they be due to the changes in the stock itself or to fluctuations in the environment. The foreseeable means of dealing with this problem are listed in the right-hand part of the diagram, and will be discussed under the heading, "Recruitment research."

At uniform availability and with no competition between units of gear:
 Relative abundance = catch-per-unit-of-effort; and
 number of units of effort =
$$\frac{\text{Catch}}{\text{Catch-per-unit-of-effort}}$$

VITAL STATISTICS

Source Data

Total catch. - The basic data for this central branch of research are the experiences of the fishermen themselves. Their "Total catch" is needed indirectly to derive "Intensity of fishing." It is used also to compute "Vital statistics," a connection which is not shown in the diagram. These statistics are collected by the several Pacific Coast States and the Province of British Columbia as a matter of administrative routine.

Boat operation. - Records of activity, particularly of the time spent fishing, would be invaluable for computing "Catch-per-unit-of-effort," as it would permit by-passing two adjustments and would avoid an additional difficulty inherent in statistics of "Catch-per-boat-week." Unfortunately, records of boat operation are lacking except for a very small sample resulting from an observer's interviews with fishermen. Whether or not these interview-data may be pressed into service in lieu of more complete operational records remains to be seen.

Boat-catch-records. - For the time being, the records of individual daily landings by fishing boats, are the main reliance in deducing changes in abundance or in availability of the pilchards from time to time and from place to place. These records collected by the State and Provincial Governments, give only the quantity of sardines in each delivery to the processing plants. In California, each delivery represents one night or a fraction of one night of fishing, in the Pacific Northwest, from a fraction of a day to several days of fishing. In neither region is there any record of nights or days spent in fruitless effort.

Length samples. - "Length samples" cover the measurements and designations of sex of a sample, usually 50, of individuals, from a delivery of sardines. In California, prior to the season of 1941-42, semi-weekly samples from 5 deliveries were taken by the California State Fisheries Laboratory. Since then, daily samples up to ten in number were taken by the California State Fisheries Laboratory at San Pedro and Monterey and by the Fish and Wildlife Service at San Francisco. Supplementing these are special series of 100-fish samples collected by the Fish and Wildlife Service at San Francisco and Monterey daily over certain periods during the three seasons prior to 1941-42. In the Pacific Northwest, sampling has been somewhat less systematic. In British Columbia, the Fisheries Research Board of Canada has taken one 100-fish sample as nearly daily as feasible. In Washington, the Fish and Wildlife Service in some seasons and the Washington Fisheries Department in others have collected one to several 50- to 100-fish samples daily. In Oregon, the Oregon Fish Commission has taken one to several 50- to 100-fish samples sometimes daily and sometimes intermittently.

Scale samples. - Beginning in 1941-42, scale samples have been systematically collected from ten fishes in each length sample by all of the agencies engaged in sampling. During three prior seasons similar samples were less regularly obtained by the Fish and Wildlife Service and in these and earlier seasons some scales and otoliths were gathered by the California State Fisheries Laboratory in California and by the Fisheries Research Board in Canada. The utility of these earlier collections is dubious but is now being surveyed by the Fish and Wildlife Service.

Analysis

Catch-per-boat-week. - The processes described under this heading have been devised for handling the California statistics for the seasons, 1932-33-1940-41. Modifications will be necessary for use with data for the Pacific Northwest and for other periods in California. The accepted manner of computing the catch-per-boat eliminates two sources of variability that are extraneous to fluctuations in abundance or availability, namely: variations in number and in the type of size of boats fishing. This is accomplished by comparing a boat's performance during two separate periods. The resulting pairs of relative catches are combined by averaging to represent fleet performance, and combined by linking to form a time series. Because the opportunity to fish is variable, depending on the duration of the moonless portion of the night, the statistical series have been divided into lunar periods and each lunar period into four lunar weeks. Year-to-year ratios are then computed between pairs of homologous lunar weeks. However, this statistic still contains several extraneous sources of variability. One is the varying amount of idleness of boats, assumed to be fishing, but actually in port on account of repairs to machinery or gear and of miscellaneous causes. It has been assumed that this is random in occurrence, and has no trend effect; and lacking any record, no account of it is taken in the computations. Two other sources of variability are treated below.

Adjust for efficiency. - There may be changes in efficiency connected with the skill of crews and modifications of gear. As yet no means has been devised of dealing with such variations.

Adjust for weather. - By computing regressions of average daily catch per boat according to weather conditions a relation between the two is derived and used as an adjustment factor. The effect of variation of available fishing time each night is also incorporated in the regression systems.

Extensive experimental analysis of wind movement as recorded by anemometer at such meteorological stations as were available, has led to the discarding of this source of weather data. Instead, the wind movement is deduced from barometric gradients in a manner which gives a representation of conditions over an extensive sea area adjacent to each fishing port. Direction as well as force is correlated with catch, and both enter into the adjustment. Other elements such as fog and precipitation appear to have no statistically consistent effects on the catch, probably because conditions at the observation points differ too much from those on the fishing grounds.

The weather adjustments already computed have measured the effect on daily catch-per-boat as an 8-season average effect and, while reliable over a long period, are not accurate for short periods of time or for specific days.

Adjust for limits. - Processing plants, at times, have limited the amount of fish receivable from a boat. Under these conditions, compliant boats stop fishing when the limit is approximately attained and the average catch must be less than if there had been no limit.

The adjustment for the effect of limits, however, is based on the assumption that their principal effect is to shorten the period of fishing per night. When a limit catch is attained by a boat early in the night, that boat's fishing effort should be figured as only a fraction of a night. This may be computed as the ratio of the actual, to the total available, fishing time.

Account is taken of boat-capacity, as well as imposed, limits. The time of attaining limits is recorded only for the catches of boats whose skippers are interviewed when a sample of fish is taken. This is only a small fraction of the whole number but it is assumed that the average time applies to the entire fleet. Due to the smallness of the sample, the adjustment is computed as an average for an entire lunar week. It is probably reliable for long, but not for short, periods. Complete operational records for the boats would be better if these were available.

Convert weight to number. - Catch statistics are always in terms of weight, but data must be in numbers of fish for computation by the methods of vital statistics. As the relationship of weight to number fluctuates in accordance with size-composition, the conversion is made on a daily basis. From a predetermined length-weight relationship, the average weight of fish in the day's length-frequency distributions is computed and this average weight divided into the pounds-caught-per-boat-day, converting that statistic into numbers-caught-per-boat-day. For samples taken in 1941-42 and subsequent seasons, the average weight is determined by direct weighing of each sample.

If now, we were to weigh each day's frequency by each day's numbers-caught-per-boat-day and sum the frequencies for all ports and all days for each season, the resulting curves might be taken as representing the relative abundance of each size of fish for the series of seasons and the task of converting catch statistics into stock statistics be considered complete.

Indeed, Hodgson (1939) regarded this very process, less some of the adjustments, as giving the relative abundance of each year-class in the East Anglian herring fishery. To use an analogous method for the Pacific sardine would be to assume either that: (1), The average boat's fishing capacity was equal in the fleet of each port, or that an equal proportion of the fish population was drawn upon by each port; and (2), the various sizes of fish were available randomly from each port, or that the length of time a complex of sizes of fish was available at each port was proportional to the population. However, these assumptions are either known or suspected to be erroneous. Various further devices of weighting, selection, and combination need be employed.

Adjust for aggregation habits. - If a series of samples taken at a particular fishing port be compared as to size-composition, it is apparent that among them there are samples that resemble each other sufficiently to have come from the same population but differ enough from certain other samples to indicate that the latter must have come from different populations. Since the various samples come from different schools it appears that certain groups of schools have a uniform pattern of size-composition and, if so, they must have been associated for a significant period of time during which their reaction pattern was the same within, but different between, the groups of schools. This corresponds to views expressed by W. F. Thompson (1926 p. 163): "Catches of a certain type, or 'runs' having certain characteristics, prevail for varying periods of time, and each of these periods is a variable unit itself." Our view differs only in supposing that there may be simultaneous occurrence of different types of "runs," -- a possibility doubtless appreciated by Thompson or one that certainly would have been, if the fishery of a given port had spread over as large an area, then as now. It will be convenient to refer to what we have called "groups of schools" and what Thompson has called "runs" as school-groups.

Obviously the population fished from a given port is not randomly distributed as to size. Unless the period of time each school-group is "available" to the fishery is either: (1) Random or (2) proportional to the abundance of each school-group, our sampling system, even though "stratified" as to time, and even though weighted according to catch-per-boat in the time strata, cannot faithfully represent the population of school groups fished from that port during a fishing season.

The summation of such weighted samples would weight the sizes in accordance with the frequency or length of time the school-groups dominated by those sizes were fished by the fleet. Since the length of time the school-group is present and available on a ground is more likely to be associated with its reaction pattern and the fluctuations in oceanographic conditions than with the relative numbers of fish represented by each school-group, such weighting would represent largely availability rather than abundance of fish.

At the present time (spring of 1942) means of distinguishing school-groups are being developed. Methods of employing the school-group idea in adjusting samples will have to await analysis of the occurrence and persistence of school-groups. It may lead to a method of weighting in school-groups or of combining samples in certain manners or may merely serve as back-ground information for appraising the validity of methods based on other principles. Since methods are still uncertain the rectangle labeled "Adjust for aggregation habits" has been related to the main line of procedure by a broken line.

Compute seasonal weights. - Apart from the departure from random distribution of school-groups within short periods of time, there is an even greater difference between the fall and winter populations in California, especially in the seasons prior to 1938-39. The fall fish are predominantly young adults, 3 to 5 or 6 years of age; the winter fish, old

adults over 5 or 6 years of age. Usually the fall season has been longer than the winter season and direct summation of samples would heavily weight the young adults. Judging from preliminary computations, which indicate greater abundance - more marked a decade or more ago than at present - in the winter when the old adults are dominant, weighting in the opposite direction would be more appropriate. Obviously, these phenomena need be taken into account in combining the samples for the two parts of the fishing season.

Compute regional weights. - The sardine at different ages tends to frequent different places along the Pacific coast (F. N. Clark 1940 pp. 44-46). In general, smaller individuals prevail in the south and larger ones in the north, with many exceptions in detail. Hence, the fishery at any one port does not afford a true cross-section of the entire population. To get that, samples from the different ports must be combined in proper ratios. Logically they should be weighted in proportion to the fraction of the total population available from each port. As these fractions differ from one part of the season to another, and in any case are difficult to determine, the computation of regional weights is no simple task.

In general, the basis for such weighting might reasonably be the estimate of relative abundance provided by the catch-per-boat-week. But the method by which this statistic has been computed uses a different yardstick at each port. That standard must be calibrated by some kind of determination of the relative fishing capacities of the boats in the fleet of each port. This project is under development but has not been advanced to the point where its usability is assured.

Another measure for determining the weighting for each port might be derived from the statistical analysis of tagged-fish returns. It would depend on computing the proportional amount that tagged fish are diluted by release in the population of each fishing region. Certain difficulties common to many tagging computations have so far prevented its use; but its desirability is indicated by the broken line running from "Statistical analysis" of the tagging procedural line to "Compute regional weights."

Combine samples. - At present, alternate ways of combining samples are under consideration. The first and simplest plan assumes that the weightings have fully discounted variations in availability so that a simple summation of weighted samples will suffice to give seasonal frequency distributions that will portray relative abundance of each size class and show the relative abundance of all commercial sizes from one season to another. As before stated, however, there is reason to distrust this assumption and unless further considerations dictate otherwise, an alternative will be adopted.

The second plan does not require assumptions as to whether the weighted samples represent relative availability or abundance. It is designed to provide an adjustment converting availability to abundance that will not produce erroneous results even if availability is not a factor to be discounted. In essence, it is a method of selecting among the weighted samples

for all sampling days at all ports the ordinates for each size-category which most nearly represent homologous levels of availability. The method takes its form from the idea that each size-category is present in varying degrees of availability to the fishery from time to time and from place to place throughout the extent of the fishing grounds. If then, the weighted, sample-day frequencies correctly portray the availability of each size-category, then, for each size-category a frequency distribution of ordinate heights will describe the number of times this size-category occurs at various levels of availability.

The problem then is one of selecting from these ordinate-height frequencies the ordinate classes representing homologous levels of availability. Theoretically, it would be desirable to have a selection that would represent maximum (or 100 percent) availability of each size-category. This would require selection of the maximum ordinate among the whole collection of ordinates for a given size-category. But the ordinate heights contain two important sources of variability apart from availability: errors introduced by weighting factors and those introduced by the random departures of numbers in each size class from the true number in the population from which drawn. Therefore the maximum ordinate in many instances would, by chance, be above rather than at the maximum level of true availability. To avoid this it has been decided tentatively to take the ordinate class at the ninth decile position. In other words, we would derive a frequency curve which represents the 90 percent level of apparent availability of each size. For the reasons just stated, this level of apparent availability may be very close to the 100 percent level of real availability.

The first plan requires that availability of each size-category have the same pattern from year to year, the second requires merely that at one time or another during the season the levels of availability of the several size classes approach their maxima. It appears that the latter involves a more conservative approach. It is to be expected that knowledge of aggregation habits, leading to the classification of school-groups, will provide important modifications in, or appraisals of, the proposed methods.

Determine length frequencies of year-classes. - Assuming that one plan or another has produced a properly weighted combination of samples to represent the stock in the sea, there remains the problem of converting each season's length-frequency, into an age-frequency, distribution. Its solution, for the years prior to the beginning of routine scale sampling in 1941, involves the use of certain statistical constants derived from scale readings.

By this is meant determination of the parameters of the length-frequencies of single age-groups or year classes that will define the shape of the frequency curves in sufficiently general terms to be applicable to years other than that in which the scales are collected. So far the only parameter we have worked with is the standard deviation, as a function of age, assuming each age group to have a normal distribution of lengths. While apparently reliable results are obtained, there is evidence

that skewness may be introduced by selective availability of the fish or by fisherman selection in favor of largest members of young year-classes, or, in certain localities, converse selection of favored small fish. It may be necessary to include a skew factor to some extent. There also are indications of multimodality in the length-frequencies of individual year classes. Whether this is sufficiently pronounced to require statistical recognition remains to be seen.

Determine growth rate. A growth curve or curves is needed to give another parameter, the mean or modal size, of the frequency distributions of year classes. Having age readings made in any one year it is simple to establish a growth curve, but such a curve would be a true one for only that year. There is evidence that growth differs from year to year, from year-class to year-class, and, more disturbing still, it appears to differ by fishing areas. For instance, a given year-class has a lower modal length in the San Pedro, than in the Monterey area. We are faced by the dilemma of using either a general growth curve fitting no specific situation, or a variety of curves to fit situations that are largely unknown. It remains to be seen whether there is sufficient regularity in geographical or annual variations to permit age determinations of recent years to be applied to the length data of former years.

Convert length-composition to age-composition. - The translation of a length-frequency curve to an age-frequency curve has proved unexpectedly difficult. As may have been anticipated from the previous discussion of parameters, the only method so far found to be applicable is that of discovering what combination of year-class length-frequencies will fit a season's length-frequency. The fixing of two of the parameters, standard deviation and mean, leaves only the third parameter, relative area, to be varied in the curve fitting. Even so, it is a laborious process by the trial and error method, but as yet we know no other. Furthermore, error in either of the two fixed parameters very seriously affects the results. In other words, the problem should be approached with extreme caution.

An expedient that greatly facilitates the process may be employed in certain situations where one is justified in the assumptions: (1) That the year-classes were of uniform initial numerical strength and (2) that they experienced uniform annual mortality since becoming of commercial size. These assumptions are approximately justified in dealing with a length-frequency distribution of fish pooled from a considerable number (enough to "average out" inequalities in initial year-class strength) of contiguous seasons during which the fishing intensity was nearly enough constant to have produced nearly uniform mortality. This severely limits the combinations of frequency-curve areas and a unique fit is soon discovered. The goodness of fit serves as an indication of how nearly the assumptions were fulfilled, except that uniform trends through the series, either upward or downward and in either year-class strength or intensity of fishing, would not be revealed by poorness of fit.

Abundance and age composition of stock. - When the weighted, combined, length-frequency distribution has been converted to age-frequency we have a series of season's curves representing the relative abundance of each age of fish in the stock. These are useful in deducing the relations between abundance and spawning and between abundance and competition effects. This is indicated by broken lines in the diagram and will be discussed later. At the moment we shall pass on to determination of mortalities and recruitments.

Compute "Vital statistics." - By vital statistics we refer to recruitment and mortality, the fisheries counterpart of the actuary's births and deaths. One might also use the term "population dynamics." The computations involved are adapted from methods previously developed or employed by Baranov, 1918; Thompson and Bell, 1934; and Ricker, 1940.

Total mortality is readily computed in situations where recruitment and mortality can be reasonably assumed to have been uniform during as many years (prior to the year in question) as there are ages present in the stock. Then, it is necessary to have only one season's age distribution, for each age class will be a constant percentage less numerous than the next younger. The constant percentage then is the annual mortality rate.

Such simple situations are rare, but, fortunately, they are not the only ones amenable to analysis for mortality. That statistic may be readily deduced from the age frequencies of two successive seasons, providing that they truly represent the stock in the sea. Here the decline would be measured by the relative numbers of a given year-class in the two frequencies and the percentage reduction of a year-class from the first to the second season would represent the annual mortality rate. If all year classes have been fished with equal intensity, hence have suffered equal catch mortality, and also have experienced equal natural mortality, the indicated total mortality will be sensibly equal for all but the "entering" year classes. Inequalities, therefore, may be ascribed to age-selective, natural mortality or age-selective fishing intensity. Correlation of the absolute quantities of each year-class in the catch with their respective mortalities should distinguish between these two age-selective processes.

Recruitment. - As used herein, recruitment means the number of sardines reaching commercial age each year. Given age-distributions that reliably represent the abundance and age composition of the stock, the recruitment is directly proportional to the numbers of individuals in the year-class that has, for the first time, appeared in the commercial catch. The only complicating feature is that there has been nothing in the previous adjustments to insure that the entering year-class will be fully represented if, in its first season, it is only partially available to the fishery. Hence, in this respect, we cannot consider the weighted curves as reliably representing the stock. However, from a series of age-distributions it should be possible, without great effort, to distinguish the age at which a year-class becomes fully available, deduce

further its percentage availability in previous years, and so arrive at a numerical evaluation of its relative strength at commercial age. Indeed, trial computations have practically proved the feasibility of this calculation.

Natural mortality. - In computations so far undertaken we have assumed the probability that mortality from natural causes is constant. This greatly simplifies the calculation of catch mortality. However, this assumption should be examined critically and perhaps revised if it is discovered that predators (other than man), and therefore predation, has increased or decreased to an important extent in any two periods under consideration.^{2/}

Also the probability of death from natural causes may vary with age, and the formulations may need appropriate revision. These eventualities cannot be appraised until a series of age-distributions, properly representing the sardine stock, become available.

Catch mortality. - While remaining aware of the possible necessity for revising the assumption of constant natural mortality, it is convenient to employ this assumption to simplify the computation of catch mortality. Given two periods, in one of which the intensity of fishing was greater than in the other, there is a unique combination of differing catch-mortalities in the first and second periods and of constant natural mortality for both periods that will account for the total mortalities and the total catches in the two periods, respectively. The mathematical formulation must take into consideration that the natural and catch causes for death are operating simultaneously and, therefore, complete with each other for the lives of the fish. It also involves consideration of whether an increase in fishing intensity, i.e. the employment of more effort or gear, brings in competition between fishing units. That is difficult of appraisal for the sardine fishery because addition of boats may as easily produce an effect the opposite of competition, i.e. cooperation, through extending the scouting area and communicating information on the location of schools. The effect of cooperation has been neglected in the computations so far contemplated. It should be taken into account, and probably will be, as soon as a method of measuring it can be devised.

^{2/} It may be possible in such a case to regard the sardine as having a number of predators, including man, and base the formulation on the effects of the simultaneous probabilities of death from the several categories of predation. The mathematics would be complicated and probably require data on more than two seasons, especially if a multiple correlation method were employed, but should be feasible, given an adequate quantity of data of reasonable reliability.

On the other hand, it will probably be safe to regard competition between gear as negligible, a point of view that is tenable if cooperation is the effective result of increasing the number of boats and also if the schools of sardines are so widely distributed that instances are relatively rare wherein a boat is prevented from making a catch by the pre-emption of space by another boat.^{3/} We do not consider in the category of competition the situation where the probability of catching a school of sardines has been reduced by the number of schools taken out of that locality previously. This is a phenomenon of reduction of the stock by catch mortality. It is taken into account by appreciating the distinction between average abundance and initial abundance in any particular period of time. (See Ricker 1940 p. 45).

RELIABILITY

Having computed one set of values on natural mortality, catch mortality, and recruitment, one gains a general idea of the magnitude of each, but the result cannot by any means be considered a determination. The various computations and adjustments have contributed errors. Also the original data had variability which perhaps was increased rather than diminished by the subsequent treatment. The mathematical result, therefore, has a probability of differing from the true value by an amount which cannot be known from one set of values alone.

In a series of sets of values, however, from which one might compute a regression, say, of catch mortality on fishing intensity, the spread of values around the regression line would give a measure of variability and one could be said to have really made a determination if that spread is small in relation to the magnitude of the observed change in catch mortality.

While this would appraise the random error, it might not detect even a large amount of error consistently above or below the true value for the entire series. Such an error might easily be introduced by simplifying assumptions or by failure to take into account certain sources of consistent bias or selection. It could be detected only by computing the same statistics by an entirely different method and from a distinct source of data. The tagging technique affords such a method and utilizes a considerably different set of original data, although, to the extent that the same commercial catch is involved, errors in fishermen's sampling may be in the same direction as in the other method.

^{3/} Persons familiar with the fishery might say that such instances are common rather than rare. It is true that there often seems to be a race between two or more boats to set their seines around the same school. This may actually take place at times, but more often a boat, preparing to make a set, betrays its intention by its actions, and so leads other boats to come to the same spot. They do so, not necessarily in the hope of beating the original boat to the school it has sighted, but in the hope, often realized, that other schools are to be found in the same vicinity. All such instances should be classified as cooperational rather than competitive. Under the latter category, there should be included only the cases where two boats independently locate and try to set upon the same school. Such cases of true competition probably are not more numerous than would serve to offset the contrary element of cooperation.

TAGGING RESEARCH

Tagging has been extensively practiced by the California State Fisheries Laboratory, and the Fisheries Research Board of Canada; also to a lesser extent, by the Oregon Fish Commission and the Department of Fisheries of Washington. Having been an interested spectator rather than a direct participant, my discussion may suffer from lack of familiarity with this technique, which is simple and direct in principle but difficult and complex in its application.

SOURCE DATA

Tag fish. - The tagging operation itself needs little discussion but various aspects of the process require attention in subsequent adjustments of the data. It may be remarked here, however, that the tags are of metal and inserted into the body of the fish following in general the method first developed by Rounsefell and Dahlgren (1933). They are recovered by electro-magnets installed in the fish-meal line of the reduction plants. The fish to be tagged are obtained, for the most part, from commercial fishermen and are subject to the same selections that influence the raw materials used in the vital statistics method. Since the numbers of "samples" tagged are fewer, the danger of non-random selectivity is greater.

Tag mortality. - It is known that tagged sardines suffer high mortality from the operation itself or from the attendant handling. The only sources of data on the magnitude and variability of tagging mortality are: (1) A limited number of experiments by the California State Fisheries Laboratory in which tagged fish were held in live cars for direct observation, and (2) a correlation establishing the relation between length of time of confinement before tagging and the subsequent returns.

The live-car experiments proved that mortality is high and variable, that small sardines suffer greater mortality than large ones, and that the size of the tag affects the rate of mortality. It is, of course, difficult to perform a sufficient number of such experiments to establish a reliable mean mortality. Moreover, there is uncertainty as to whether the difference in treatment received when the fish are released in the live-car rather than directly into the sea (as in the regular tagging operations) has caused the live-car mortality to differ from that in the sea releases. This uncertainty is especially acute with respect to liberations in the Pacific Northwest, where tags have been applied with a different instrument (tagging-gum) from the scalpel and forceps used in California and where the fish were tagged directly from the fishermen's seine instead of being brailled into a holding net for tagging; and, also, where the roughness of the sea generally imposed more difficult conditions for the handling than in California.

Recover tags. - Since sardines are handled in bulk and mostly by machine, few tags would come to light without a specific recovery system. That now in use consists of magnets installed in the meal-lines at canneries and reduction plants. Difficulties arise in achieving installation

of magnets in all plants, and in connection with their effectiveness when installed in different mechanisms and under different operational methods.

Test magnets. - This requires that each installation be tested to determine its recovery efficiency. Periodic tests of the same installations are made to discover fluctuations in performance and detect any changes that may occur as plant operations are altered. The test consists of mixing a definite number of tagged dead fish with an ordinary lot destined to go through the reduction system and recording the percentage of tags recovered from the magnet. A possibility that the efficiency of recovery of test-tags may differ from that of tags in sea-released fish arises from the fact that the former lie within the body, unattached to the tissues, and not far from the open, insertion incision; whereas the latter are encysted by tissue and the incision healed shut. It is likely, therefore, that the efficiency may be somewhat over-rated by the tests. On the other hand, a few recovery experiments indicate a lessened efficiency of recovery from fish destined for canning than from those destined to go directly to the reduction machinery. This is probably due to the loss of tags from the body cavity in the cutting and eviscerating process. The performance of testing experiments in connection with canning operations has met with obstacles preventing the accumulation of sufficient experience to gauge the reliability of efficiency ratings. Their value for adjustments is also lessened by the custom of mixing whole fish with cutting offal in the ordinary operating procedure. In all, the efficiency of recovery varies widely and while important for our calculations is difficult to determine.

Analysis

Adjust for tagging mortality. - Two basic adjustments are made to deduce the actual number of viable tagged fish released. The first utilizes the live-car experience in adjusting release records downward by the indicated amount of mortality induced by the tagging process, with due regard to the size of the sardines. The second takes into account the additional mortality brought about by the increased time of holding to which the late-tagged members of a given batch of fish were subjected. It involves establishing a regression of returns on serial order of tagging in blocks of 100 or other suitable number of individuals for each batch or group of batches of fish tagged. These regression values adjust not only for the time-connected differential mortality within a batch but also for the differences in mortality between small batches tagged in a short time and large batches requiring more time for tagging.

These adjustments have been employed in the analysis of returns from California-tagged fish, but no comparable methods are available for those tagged in the Pacific Northwest, though it would appear that the second adjustment at least would be feasible for releases in that area.

Adjust for recovery efficiency. - This adjustment applies the magnet efficiency records and also incorporates a calculation taking into account any amounts of fish run through plants when or where magnets were not in operation. To some extent a differential adjustment for recoveries from reduction of whole fish and reduction of canning offal is feasible from a comparison of returns from the two categories wherever plant records permit segregation. Since canning is not practiced in Washington and Oregon, this feature is not a problem there, but it exists in British Columbia as well as in California.

Adjust for intensity of fishing. - One essential statistic sought through the tagging technique is the catch-mortality. If it were possible to release all the tagged fish immediately prior to the fishing season and if they were immediately distributed at random through the commercially-fished population, this statistic would be the ratio of first-season returns to the number tagged. Another essential statistic, total stock, could then be computed simply by the proportionality:

$$\frac{\text{number of fish tagged}}{\text{total stock}} = \frac{\text{number of returns}}{\text{total catch}}$$

but tagging can be done only at intervals during the fishing season and the tagged fish probably diffuse only gradually through the general stock. Hence, first season's returns are almost useless and it is necessary to deduce from subsequent years' returns what the first year's returns would have been under the simple conditions described above. That deduction is made by extrapolating back to the first year a line representing the annual rate of decline of tag returns. Since the annual returns depend in part on the amount of fishing done, some adjustment must be made when the amount of fishing changes during the series of years included in the tagging experiment.

The adjustment used for the California statistics has been to compute for each season the number of returns per unit number of fish caught. An identical adjustment would be feasible also for the Pacific Northwest tagging returns. While this adjustment may suffice for useful approximations, it obviously gives identical treatment to a fluctuation in catch whether due to a change in the amount of fishing or in abundance of the sardines. Yet these two phenomena have different effects on the returns. Furthermore, the fishing in a current year, by removing a certain number of tagged fish, influences the returns of subsequent years. Except therefore, in situations where it may be safely assumed that the fluctuations in catch have arisen only from moderate and random changes either in intensity of fishing or in abundance, this adjustment may require revision. Where a trend exists in fishing intensity or in abundance there would be particular likelihood of erroneous results. Such cases would require additional adjustments appropriate to the particular circumstances, and possibly materials from the vital statistics methods could be drawn upon for such analyses. This has not been indicated in the diagram.

Statistical analysis. - As explained in the previous section, the statistical analysis of tagging experiments depends mainly on a line (or curve) representing the trend in annual adjusted returns. The intercept of the line at year one (an extrapolation) is used to compute catch mortality. By another computation, it also results in estimate of total commercial stock. The rate of decrease in annual returns is taken as the total annual mortality. The remaining statistic, natural mortality, is derived algebraically from catch mortality and total mortality.

Since the trend curve is based on returns during a series of years, the statistics resulting therefrom, represent the conditions, not in any one year, but are an average (not necessarily an arithmetic mean) for the series of years.

It has already been pointed out that the adjustments, particularly that involving the size of the catch, may have affected the data in a way that calls for modification of the above-described computations. Instead of that, determination for a number of periods of overlapping years might point the way to an interpretation or correction of the statistics for individual periods or even individual years. Thus far, however, records are available for only two periods and these possibilities cannot yet be examined.

A further aspect of the computations so far made is that when Pacific Northwest catch and Pacific Northwest returns of fish released in California are excluded different rates are indicated than when they are included. This points either to the non-availability to the California fishery of at least a portion of the stock that migrates seasonally to northern waters or to some discrepancy of experiment or analysis so far unrecognized.

Fortunately, there is reason to believe that many of the difficulties of interpreting tagging results may disappear or be resolvable as more data accumulate.

The value of the tagging method as a largely independent method of determining mortalities cannot be over-emphasized and it is particularly encouraging that the computations have led to determinations practically identical with those resulting from a preliminary application of the method of vital statistics.

At the same time it should be emphasized that both the tagging, and the vital statistics, methods depend, in the last analysis, on the representative nature of the sample dealt with. At its present stage of development, the method of vital statistics includes a much larger sample, better distributed in time and space and more thoroughly adjusted to exclude the effects of extrinsic influences than does the tagging method.

RECRUITMENT RESEARCH

Determination of the amount of recruitment would be an outstanding achievement, but would be, of itself, of only limited usefulness so long

as nothing is known as to which of two major influences determine its value. These influences are those: (1) Not connected (let us say, extrinsic influences); and (2) connected (i.e., intrinsic influences) with the size of the sardine population itself. The first category would include hydrographic and oceanographic conditions that may influence the amount of spawning and the survival of young. It would also embrace competition with, or predation by, other marine animals. The second category would include the direct influence of population numbers on the amount of spawn produced and the competitive effects of population numbers on the number surviving. The amount of spawn would be directly, and the amount of survival inversely, proportional to population numbers. The survival rates might be different for the various stages of young.

So far as intrinsic influences are concerned, one would expect recruitment to be small even at low levels of fishing intensity where there is a very large spawning population and also a very crowded condition which could impose a high mortality. At intermediate levels of fishing intensity there would be maximal recruitment resulting from a still large spawning population and the low mortality associated with an uncrowded condition. At extremely high levels of fishing intensity there should again be low recruitment due to a very small population producing insufficient spawn for maximal recruitment even in a very much thinned-out condition where competition within the population would result in negligible mortality.

If the intrinsic influences were operating alone, it would be a simple matter to construct a curve of recruitment according to levels of fishing intensity by merely observing what happens to recruitment over a range of fishing intensities. But the extrinsic influences, operating simultaneously also affect the recruitment. For instance, preliminary analysis of vital statistics for two periods of the sardine fishery showed that quadrupling of fishing intensity was accompanied by doubling of recruitment. The earlier period with the low intensity of fishing covered 8 seasons, and the later one of high intensity, 4. Both periods were thus of sufficient duration to have had a variety of extrinsic influences and their effects on mean recruitment should to some extent "average out." Yet one would be bold to conclude that they had indeed averaged out and that the increase in recruitment was in fact due to the increased intensity of fishing. On the contrary, one could almost as easily argue that through the later period, there had been 4 years of favorable extrinsic conditions that were responsible for the increase.

Yet a choice must be made between the alternatives. If the increased recruitment were in fact due to the thinning out of the population by intensive fishing, then this high rate of utilization, with the attendant large annual catches could go on with no ill consequences other than a not intolerable reduction in average size of fish. But if it were due to a lucky run of good survival years, the present rate of fishing could

not go on without serious diminution of the population, resulting in both markedly lower annual catches and a marked and perhaps intolerable decrease in average size of fish.

At the moment there is no basis for making the choice, but the program charted in the right-hand portion of the diagram, facing page 1 which is now to be discussed, is designed to distinguish between the effects of the extrinsic and intrinsic influences.

Source Data

Egg and larvae samples. - By a plankton-collecting program designed to sample the egg and larval pilchard population in waters of the spawning region, it is planned to obtain material for two sets of data on each season: 1) The numbers of eggs spawned and 2) the survival of the larvae to the post-planktonic stage.

To serve these purposes, quantitative collections of eggs and larvae must be made. Features of quantitative technique so far employed in this branch of the program are use of: The oblique method of towing to sample all egg-and-larva-bearing strata; current meters in the nets to measure the quantity of water strained in each haul; regular pattern of stations; and regular periodicity in making collection. Additionally, there have been special collections or special methods employed in the regular collections to test the reliability of the tow-net method for sampling eggs and larvae. These special inquiries have convinced us that quantitative work is feasible, if also difficult. Some of the techniques still have to be improved.

Hydrographic and meteorological data. - Observations on hydrographic conditions taken simultaneously with the collection of eggs and larvae, are intended to provide a record of conditions to be correlated with the time, place, and volume of spawning and with the survival of larvae. It is already known that the dominant features of oceanic circulation along the west coast, and particularly the maintenance of fertility of the waters through the upwelling process, are connected with the winds. With the establishment of the relationships of the oceanographic features to the meteorological influences, on the one hand, and to the amount of spawning or to the survival of larvae, on the other, it may be possible to establish directly the relationship of amount of spawning or survival of larvae, or both, to the meteorological conditions. Hence simultaneous observations on hydrography, meteorology, and the young stages of sardines promise to elucidate the influences on recruitment.

The particular oceanographic observations so far programmed, include: Those on temperature and salinity down to 500 meters regularly, and pilot observations to greater depths; determination of oxygen and phosphate content for the same strata; and counts of the diatom population for each ten-meter level to 60 meters in depth. All of these observations and

their subsequent analysis are being undertaken by the Scripps Oceanographic Institution in cooperation with the Fish and Wildlife Service. Accessory experimental work on rates of biological processes in the survey area is also under way at that Institution.

Analysis

Compute total numbers of each stage. - With reliable quantitative collections of eggs and larvae at each station, it is further necessary to integrate the total numbers over both time and space. The time element involves proper weighting to account for the time interval between successive observations over the station pattern. This in turn involves certain assumptions, or preferably a determination of a curve of the volume of spawning as a time function. The integration over space depends upon a curve of distribution of the organisms in the sea area sampled. Both phases of integration are still in the developmental stages. An additional element in the computation is an adjustment necessitated by the smaller catches of larvae by day than by night.

For the time being, work will be directed toward determining total numbers of each stage in the particular area included within the egg and larval survey. This covers only a part of the spawning region. Extension to other areas must await either better boat facilities or a fortunate discovery of relationships with meteorological conditions which may provide a certain reliability in extrapolation.

In any even, the integration must be proceeded or followed by certain adjustments.

Adjust for drift. - Since the survey area is of limited extent and contiguous to other possible areas of spawning, some allowance must be made for gains in numbers by organisms drifting into the area and losses from their drifting out. This aspect is not serious with respect to eggs, which hatch in three days and, therefore, cannot drift far; but it is important in the case of larvae which may spend weeks or even months in the drifting phase. With the pattern of circulation determined from hydrographic observations, an allowance should be feasible. The principal difficulty now foreseen is the amount or rate of lateral diffusion, which would not be apparent from the circulation pattern alone. This adjustment is therefore still in the problem stage.

Adjust for rate of development. - The numbers of eggs or larvae found in each stage will vary inversely with the time occupied in passing through the stage. One occupying a short interval of time will afford a smaller accumulation of individuals than one occupying a longer period. Adjusting numbers to allow for the "accumulation effect" involves knowledge of the rate of development or of growth. This has already been worked out for the eggs, but the rate of growth of larvae has yet to be determined.

Infant survival. - Having fully adjusted the data on numbers at each stage of infant survival, its rate should be quite simply described by a frequency distribution of the successive stages. The simplest result to be expected would be a J-shaped curve transformable into a straight line by suitable mathematical procedure. Differences from one season to another in the slope of this line should register the changes in survival rate. If, however, there are variations in that rate during the larval existence, a more complex curve would result and its interpretation would be more difficult.

Amount of spawning. - There are two approaches to the measurement of amount of spawning through 1) Computations from data produced by the vital-statistics method that would effectively enumerate the spawning stock; and 2) sampling the sea water for eggs. Both have serious obstacles. The approach through spawning stock involves the appraisal of fecundity of females by sizes or ages, an appraisal rendered difficult for lack of samples of spawners which resort largely to grounds farther offshore than the area in which commercial fishing takes place.^{4/} Therefore, this approach has been indicated by a broken line in the diagram facing page 1. The approach through sampling for eggs is far simpler in principle, and in terms of the diagram would be directly from the previous computation of total numbers. However, it involves surveying larger areas than has so far been feasible with the single vessel available for this research. Satisfactory enumeration by either method depends on substantial augmentation of the sea work.

Correlations with hydrographic and meteorological conditions. - So far as recruitment is determined by the amount of spawning and modified only by the rate of larval survival, determination of the former and correlation of the latter with hydrographic and meteorological conditions would give the relationships necessary to the interpretation and prediction of changes in recruitment rate. This correlation must relate to the conditions in the one area of survey, but if it were found very exact and involved hydrographic or meteorological features of wide-spread nature, the results would possibly apply to the entire range of species. It is more likely, however, that the more complex and extended procedure discussed in the following paragraphs will be necessary.

Multiple correlation to distinguish effects of population density from oceanographic influences. - Thus far a rather simplified view has been taken - one that stresses the larval stages as the only factor critically modifying the relationship between amount of spawning and recruitment. A more comprehensive viewpoint would recognize that there are other influences and that they may be exerted at any stage of life. To illustrate this, the recruitment diagram facing page 25 is given. Instead of a procedural diagram as in the one facing page 1, this is one of mathematical equivalents and correlations.

^{4/} Frances N. Clark, 1934, has studied fecundity in material taken from the commercial catch. Her work proved the paucity of spawning-ripe individuals in the catch and also the difficulties in determining the numbers of eggs spawned per female per season.

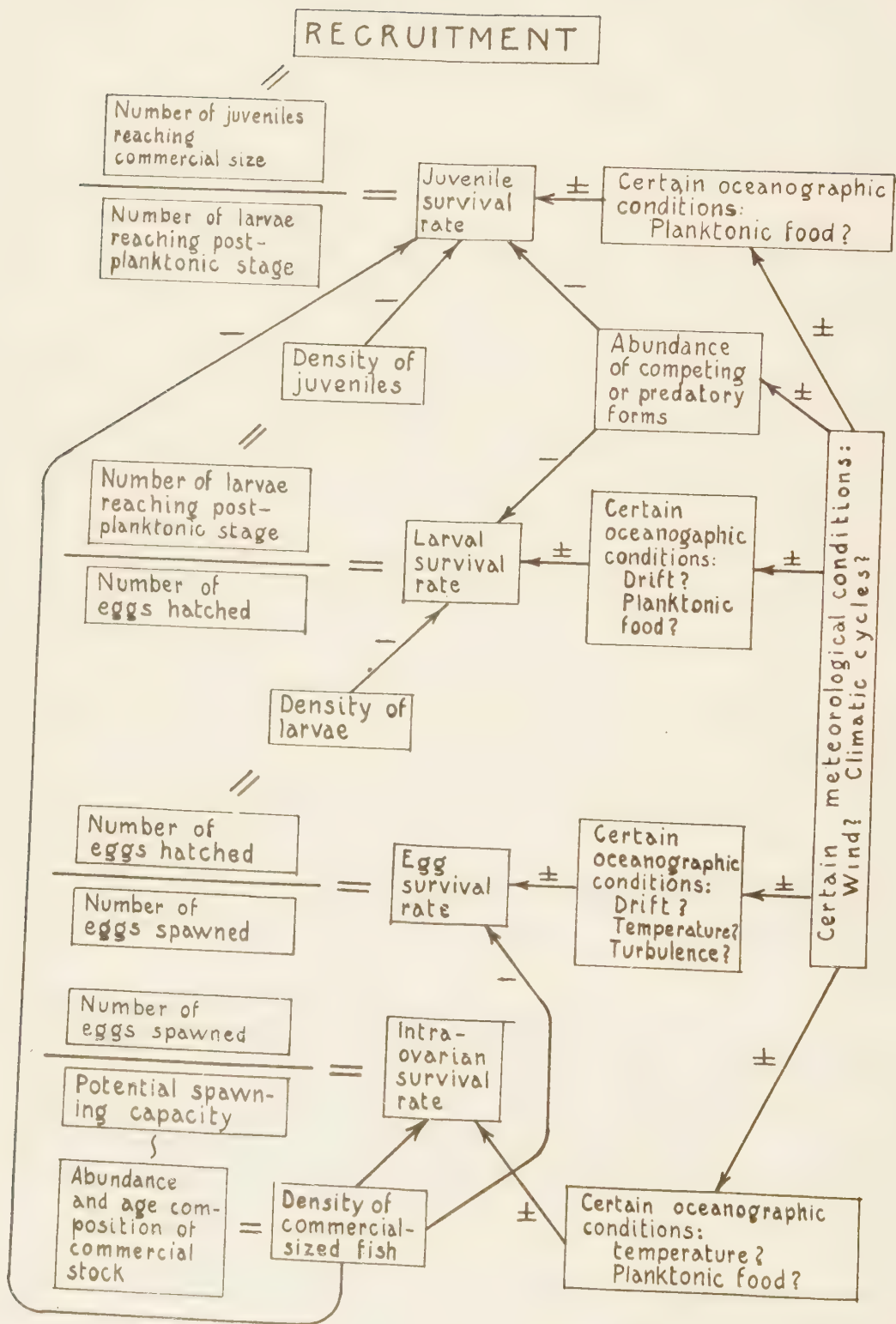
Structure of the recruitment diagram. - The diagram reads from bottom to top, beginning with the production of eggs within the female and leading through successive stages to net recruitment at the top. At the left are variables pertaining to population densities (intrinsic influences), and in the middle are the survival rates (dependent variables) upon which the two categories of influences (independent variables) operate to affect the recruitment. Algebraic notations relate equivalents. Thus the fraction "number of eggs hatched" over "number of eggs spawned" equals the "egg survival rate", and the "number of eggs hatched" also equals the "density of larvae", at least initially. Correlation notations are given as arrows pointing from the independent to the dependent variable with a sign to indicate whether the correlation should be negative or positive; and where indeterminate, i.e., depending on the way the independent variable is expressed, the plus-minus sign ($\pm$) is used.

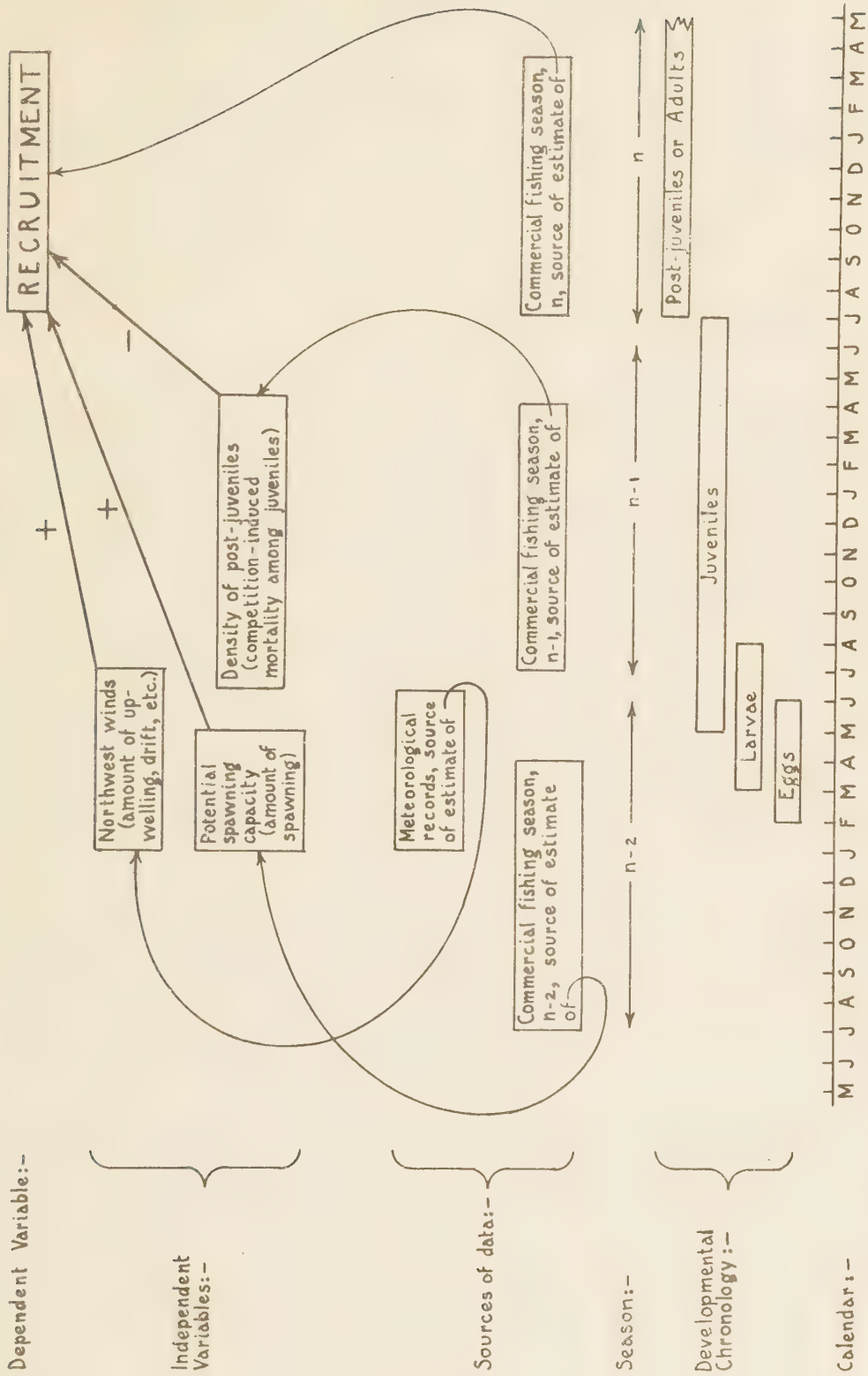
Discussion of the recruitment diagram. - It is not intended that the recruitment diagram should be an outline of procedure. Rather it indicates a complex of relationships too extensive and inclusive of too many subjects upon which data are, for the most part, non-existent at present and difficult to obtain in the future. It illustrates the manifold phases of the recruitment problem and should serve as a reminder of the fragmentary nature of less comprehensive treatments.

This comment, however, should not discourage effort to solve the problem of recruitment by some less comprehensive or abbreviated process. If the survival rate in certain stages of life is relatively constant from year to year these stages can, without risk, be ignored. If this be done and high correlation is found, much time will have been saved. If, on the other hand, the results turn out to be indeterminate, it would merely mean that the stages that were ignored did, in fact, have variability and should have been considered. Since that requires data for which there are now no collection facilities, we will merely have to decide between surveying the significance of available data or neglecting them. It is clear, however, that a program for determining additional aspects of certain reproductive attributes of the pilchard population and also of oceanographic conditions, including study of that portion of the marine fauna which may exert predation on any stage of the pilchard, should be started at the earliest opportunity.

Discussion of an abbreviated recruitment analysis. - It is interesting to speculate on how limited a view would have to be taken if one were confined to data already available or in process of becoming available. The diagram opposite gives a scheme of correlation analysis on what appears to be fairly reasonable grounds. It ignores intra-ovarian, and egg, mortality. Such sampling of eggs on the spawning grounds as has been made is impressive in the relative constancy of the numbers found and fails to suggest important variability in survival.

The scheme includes only the oceanographic extrinsic variable affecting larval survival because it hardly seems that competition between





larvae can be important as they form such a very small fraction of the plankton community. Owing to the lack of data, it ignores competition from other forms. This is perhaps the greatest weakness.

It includes only the intrinsic influence on juvenile survival and considers that the competition takes place between juveniles and post-juveniles rather than within the juvenile category itself. (This particular selection has a back-ground of observation too extensive to describe here. It was suggested by the virtual disappearance of dominance of year classes since intensification of sardine fishing took place.). With juveniles, also, the competition from other forms is ignored for the same reason that it was among larvae. However, utilization of data on predator species of commercial fishes invites attention.

The diagram opposite places the elements on a time-scale horizontally, showing the approximate season and year from which the source data are drawn and the approximate season and year in which the independent would be expected to influence the dependent, variable, recruitment. Thus recruitment of the current season (n) would be estimated from the (fully adjusted) sample of the current commercial fishing season. The numerical value of this recruitment would be correlated with: (1) The density of the post-juvenile population during the previous season (n-1) as estimated from the (fully adjusted) sample of the previous commercial fishing seasons; (2) the strength (or persistence) of northwesterly winds during the spawning and developmental portion of the second previous season (n-2) as estimated from weather records of that portion of the second previous season; and (3) the amount of spawning during the second previous season (n-2) as estimated from the (fully adjusted) sample of the commercial fishing season with, of course, due allowance for the percentage of fish that are mature and the proportionality between size of spawner and number of eggs spawned.^{5/} The curved arrows connect source data with the equivalent derived from it. The straight arrows with plus and minus signs point from dependent variables to the independent one. It is assumed that correlation between northwest winds and recruitment is positive through its influence on upwelling and the attendant "fertilizing" of the sea water. It could be negative (or curvilinear, i.e. positive in some parts of its strength or persistence range and negative in others) through its effect on drifting larvae away from the more favorable nursery grounds. Which of these actually occurs would be revealed by the correlation analysis.

The multiple correlation process indicates in the diagram opposite, three independent variables. If the correlations or regressions are rectilinear, 6 degrees of freedom would be absorbed by the multiple correlation process. It appears that data on the two intrinsic independent variables will be derivable for eight seasons when the portion of the program now in progress is completed. By that time, however, two more seasons will have elapsed and if they can be added, a series of ten seasons will be available. The meteorological data, if regular Weather Bureau

^{5/} Using approximate determinations published by Frances N. Clark, 1934.

observation will suffice, would, of course, be available for the same years. With ten seasons and the loss of six degrees of freedom there would be left four degrees of freedom on which to base judgment as to significance of results. This number is perhaps too low to do more than indicate whether the general hypothesis is on the right track. Certainly it will not be enough to conclude that the hypothesis is disproved. (Of course, correlation analysis can only disprove: it can never prove by hypothesis.)

SUMMARY

As the pilchard program now stands, two lines of evidence when the work on them is completed, will give the rates of catch and natural mortality, and the rates of recruitment over an 8-season period, 1932-3 to 1939-40, with the prospect of adding two subsequent seasons. By appropriate computation, estimates of the total size of the population and its size-composition will be available on an annual basis from the "vital statistics" approach, and also available as a mean for a group of seasons through tagging studies. This will afford estimates of the effects of fishing at different levels of intensity on the quantity and quality of the catch. The estimates will be true only for the seasons covered by the analysis. To extrapolate them so as to predict what consequences will follow any particular level of fishing intensity, a third line of evidence is needed for determining whether the recruitment has been conditioned by the size of the stock itself (and hence predictable from the "vital statistics" evidence) or whether it was affected to an important degree by oceanographic conditions (and therefore unpredictable except in terms of range of variations about a certain mean condition). This matter is being investigated. Great difficulties have been met and still others may be anticipated, but in spite of these possibilities of solution exist.

An important phase of the entire problem is whether the range of intensities of fishing, which happened to have been included in the 8 or 10 seasons under study, is sufficient to cover reasonably well the range to be anticipated in the future. The range could be extended to lower intensities by going back to the records of still earlier periods of fishing. To extend it to higher ranges would depend on developments in the fishery. To permit development to higher ranges of intensity could involve the risk of reducing the stock so far below a desirable level that recovery might be slow. Appraisal of the degree of risk involved and of the desirability of undergoing that risk will depend on the nature of the results that flow from the current program, and may well be deferred until they become known.

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2. Determination of the Age of Juveniles by Scales and Otoliths

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THE PROBLEM

Up to the present, no method has been developed for determining the age of individual specimens of the Pacific pilchard, or sardine. Lacking a satisfactory substitute, it has thus not been possible to isolate year classes of fish taken in samples of the commercial catch, so as to trace, by serial sampling, their growth in length, or to follow their passage through the fishery.

Such available knowledge as bears on the growth and age of pilchards results from the occurrence of dominant year classes in the population from time to time, which can be readily recognized by their prominence in systematically collected samples of the commercial catch. By this method it has been shown (Clark, 1936, pp. 18-24) that year classes have entered the fishery when their mode was between 190 and 200 mm., that their approximate growth could be followed through as many as five years, when their mode was in the neighborhood of 230 mm., and could be traced with somewhat less certainty, if they persisted in the fishery, for as many as five additional years, when their mode was near 260 mm. Thereafter, according to Clark's work, the hitherto dominant groups have completely lost their identity.

This statistical method is useful only for studying those year classes abundant enough to produce persistently prominent modes in the length frequency curves. However, the method does not permit determining whether a dominant group is composed of one or of several year classes, nor can it be used for studying individually or collectively the more numerous, adominant age classes. Furthermore, as Thompson (1926, p. 187) says, "...our view of the course of a given year-class is probably much distorted by the conditions of selection and by the errors of sampling."

Neglecting, for the purpose of this study, the problem of sampling, an ideal method of analyzing frequency curves would expose and recognize individual year classes from the youngest to the oldest, and of all degrees of abundance. To be accomplished this necessitates age determination of individual fish.

The desirability of such a method was emphasized by Thompson (op. cit. p. 52) who says, "There are two ways in which the abundance of fish may be affected; first by the variations in mortality rate at various stages of life preceding capture, and second by the direct effect of the environment upon the movements or habits of the fish. In the first of these the analysis for size or age must be of supreme utility, being the sole means of determining the relative proportion each age forms of the catch..."

Since the ages of individual fish are determined usually from scales or otoliths, Thompson made a preliminary examination of pilchard scales in the course of his investigation on that species (Thompson, op. cit). He used for this purpose a collection of 194 specimens, ranging from 144 to 228 mm. in length, taken from October 28 to December 2. These were

then read for age, without knowledge of the size of fish, and with frequent changes in magnification to avoid being influenced by the size of the scales. It was found that 20 percent of the scales were illegible, and 54 percent of the readings questionable. In a subsequent examination, with reference to the size of the fish, 61 percent of the readings were questionable, and 25 percent of the scales illegible. A comparison of the two readings indicated that, what with disagreements and illegibility, only about 25 percent of the total age determinations were completely acceptable. When the length of the fish at each age was calculated from the scales by Lea's method (Lea, 1913), Thompson found such discrepancies between the actual lengths of fish at the several estimated ages and the lengths at those ages as calculated from older specimens as further to discredit the dependability of reading pilchard scales. He says, then (Thompson, 1925, p. 53), "So important is the analysis by age regarded at present that it is with the greatest regret that it is temporarily omitted. We--the director and the successive assistants--have vainly attempted to read the age marks on the scales and otoliths. This does not mean that the attempt to utilize them will be abandoned. . . . we may be able to develop a method of accurately reading the scales according to the age their lengths should indicate. This attempt is already in progress." And, on p. 57, "With this simple presentation of results the use of scale readings is concluded for the time being."

No further studies were carried to completion following Dr. Thompson's preliminary report, however, and no other publications have appeared to date on this subject. Nevertheless, the possibility of determining the age of pilchards from scales and otoliths was not closed, and the belief was expressed from time to time by those studying the species that the subject must be further studied.

Accordingly, by agreement with the California Division of Fish and Game, the staff of the United States Fish and Wildlife Service engaged on pilchard research took as one phase of its program a study of the problem.^{1/} This paper, the first report on the results of that study, inquires critically into the utilization of scales and otoliths for determining ages of pre-adult sizes of pilchards; that is, those ranging from the smallest taken by bait fishermen up to those around 185 mm. in length, which is approximately the size at which 50 percent of the females become mature (Clark, 1934). In addition, somewhat less critical results are given for fish up to around 220 mm., at which size 100 percent of the females are mature.

^{1/}This study has been made possible only by the cooperation of members of the fishing industry, who aided in our collection of material. The authors are grateful to the following fishermen or dealers, who took an active interest in securing samples of the bait fisheries: Messrs. J. L. Sullivan, Eugene Sullivan, Dominic San Phillip, and Leonard Schipper at San Diego; Joe Dixon and George Dyson at Newport Beach; S. Carmen and Frank Puggleise at San Pedro; M. Martinelli at San Francisco; and Thomas A. Martin, Jr., at Seattle, Washington. The

Collection of Material

So as to determine the characteristics of an age mark and to observe the time when it forms, scales of young fish of known age, that is to say, young of the year, were studied during an 18-month period beginning with March, 1938. Material was obtained by sampling bait fisheries in southern California, which is the center of this industry, and which is probably the region of maximal spawning (Scofield, 1934). Weekly samples at San Diego, Newport Beach, and San Pedro were taken wherever they were available, i.e., in the fresh fish markets, from fishermen with whom special arrangements to save young pilchards had been made, from canneries, from bait receivers, or from the live-bait tanks of commercial pleasure boats. Enough fish were taken to total, for all localities, about 1500 specimens each week, and to average about 500 from each locality. This work was carried on regularly from March, 1938, to May, 1939. Meanwhile, to have a representation from other parts of the pilchard range, fish were obtained elsewhere by various means.

Beginning November, 1938, and extending through October, 1939, weekly samples were taken of the bait fisheries at San Francisco and Monterey. In addition, several samples from Mexico were supplied by tuna boat captains; and in July, 1938, Captain C. W. Thomas of the coast-guard cutter, Hermes, invited the senior author to accompany the Hermes on a voyage to Magdalena Bay, Lower California, where, for one week, daily samples were taken, totaling altogether 1500 specimens.

Kerckhoff Marine Laboratory of the California Institute of Technology provided laboratory facilities for the southern California station. All the staff members of the United States Fish and Wildlife Service (formerly Bureau of Fisheries) engaged on pilchard research have contributed something toward the progress of this study. Mr. Robert Luckhardt was engaged in sampling the bait fisheries in southern California and San Francisco; Mr. Ralph Silliman canvassed the possibilities of obtaining young pilchards in Washington and Oregon. Mr. O. E. Sette, in charge of the pilchard investigation, gave advice and criticism throughout the entire course of the study.

Mr. William Bowen, microscopic technician of Stanford University, supervised sectioning and staining of the scales. Preparation of the scales and otoliths for microscopic examination, subsequent clerical work on the statistical processes, and the preparation of graphs were done by W. P. A. Projects 702-3-1 and 10917, respectively. Microtechnical and clerical work was done by N. Y. A. assistants, furnished through the Stanford Student Employment Office; and Stanford University has generously provided the working quarters of the South Pacific Investigation, giving the staff free access to its libraries and other useful facilities.

Finally, we acknowledge with gratitude the critical reading of the manuscript by Dr. W. F. Thompson of the International Pacific Salmon Fisheries Commission, and Dr. Frances N. Clark of the California State Fisheries Laboratory.

Meanwhile, since it had been reported that young pilchards are taken occasionally along the Washington coast by fishermen, and appear from time to time in the stomachs of salmon caught there, one of the Service's staff, Mr. Ralph Silliman, was stationed at Seattle to secure any specimens that might be obtainable. By examining a large number of salmon stomachs and by making special seine hauls, Mr. Stilliman obtained a sample of young fish at Westport in April, 1938, and others at Tokeland, Willapa Bay, in September and October. (Silliman, unpublished manuscript.)

Altogether, 175 samples were taken, totaling 71,800 fish. For measuring, the fish were laid on a board especially designed to obviate numerical bias on the part of the operator, (Sette, 1941) and the body length (i.e., tip of head to end of fleshy part of caudal peduncle) read to the nearest millimeter. For each sample, scales were removed from the first 50 to 75 specimens having any suitable ones still adhering. Ordinarily they were taken only in an area of about 1 1/2 centimeters square centered by the tip of the pectoral fin, or, in a few exceptions, as close to that area as scales were available. They were removed with forceps, dipped in water, wiped with the fingers when still fresh to remove adhering slime and tissue, and preserved in envelopes. Otoliths were removed from most of the specimens from which scale samples were taken. These were washed in water and preserved dry in envelopes. Scales were taken from 11,500 fish; otoliths from over 10,000. Not all these were read; only enough to secure reasonably adequate representation from each month.

AGE AND GROWTH OF JUVENILE PILCHARDS AS JUDGED FROM LENGTH FREQUENCY CURVES

Because the first two year classes are each usually recognizable from older fish by their distinctive size, length frequency curves are useful for identifying the age of young fish up to two years. They therefore provide a starting point for associating age with number of rings on the scales and otoliths.

Under simple conditions such an extensive sampling as was carried on should provide a series of frequency curves truly representing the total population of young pilchards in the sea. Unfortunately, for various reasons, conditions are not simple. Judging from the protracted spawning season (Clark, 1934) and the extensive spawning range (Scofield, 1934; Silliman, unpublished manuscript), the year's brood along the coast probably consists of a number of groups of fish, each representing an individual wave of spawning in a particular locality. Since pilchards, like other species with similar habits, appear to school more or less according to size, it is conceivable that, so long as the several groups differ in size, each will travel more or less independently, entering and leaving the field of the bait fishery at irregular intervals, thus offering the fishermen only a limited availability. This effect must be enhanced by the fact that bait fisheries do not cover the entire ground

traversed or occupied by pilchards--there are no such fisheries of importance north of San Francisco, or between Monterey and Los Angeles Counties, or between Turtle Bay and Magdalena Bay, nor do the bait boats operate farther than about 15 miles offshore. In addition, the method of fishing is such that only those fish schooling near the surface are caught, while those schooling deeper are missed. Moreover, the fishermen tend to seek certain sizes; in some places the smaller fish, in others the larger, depending on local demand. For these reasons only a highly and variably selected part of the population could be available to us.

The effect of this selectivity might be partly eliminated by weighting the samples according to the catch, or according to relative abundance at the several localities, but statistics bearing on the bait fishery or on regional abundance are not available, and such weighting is therefore not at present practicable. Because the samples were of various sizes they were all weighted equally (to 1000 fish); likewise, the monthly totals of the weighted samples at the several ports (to 1000 fish); and the totals of all California ports thus weighted were summed by months. The original data were divided into two parts, as indicated by vertical lines in figure 1, the one comprising what was judged to be approximately all the youngest year class, the other the older ones. Each part was weighted separately, to 1000 fish, thus emphasizing the height of the several modes without regard to their relative abundance.

Judging from figure 1, a new complex of groups of fish first appeared in appreciable numbers in the California samples in June, in 1938, ranging in body length from about 40 to 95 mm., and having several modes, the dominant one at 70 mm. Save for a few specimens in May, fish of that size-range were not available earlier, in spite of every effort to obtain them, and were not available again through May of the following year. A fairly similar group appeared in the bait fishery of San Pedro in 1922 (fig. 2; Higgins, unpublished manuscript), showing that such occurrence is probably normal. It is probable that this group represents the youngest year class. This conclusion is based on the following considerations: in the most sinistral group of modes for June, 1938, in figure 1, there is a range of about 55 mm. This leaves only 40 mm. to the left in which to include a possible younger year class. It would be extremely unusual for the zero year class to have a narrower range than the I's; or to be less widely separated from the I's than the I's are from the II's; or for the first year of growth to be less than the second. But, nevertheless, even if there were an additional year class, then the fish in the above mentioned 40-mm. range should have grown almost, or quite past the 40-mm. point by the following May. Before that time, they should have been taken by the nets of the bait fishery, which, judging from figure 1, could hold fish as small as 40 mm. That no such fish were taken in our samples is strong evidence that they did not exist in the waters of the area studied. It seems beyond question, therefore, that the most sinistral group of modes for June in figure 1 does represent fish produced in the spawning season of 1938.

Subsequent growth can be traced by the monthly progression in the position of that group from June, 1938, through May, 1939, when the dominant mode was near 120 mm. It is evident that the year class was composed, at first, of several subgroups, the availability of which fluctuated more or less independently during the year. This accounts for irregularities in the progression.

As for the ages of fish older than 0 year class, it may be supposed that in curves to the right of those belonging to year class 0, the smallest fish, those around 84 to 100 mm., in March, 1938, were the smallest one-year olds, and may be homologous with those ranging from 130 to about 170 mm., in October, 1938, and to those of an undeterminable range above 150 mm., in May, 1939. From figure 3 it is shown that fish as small as 150-160 mm. were taken in the fall commercial fishery for "adults" at Monterey in October, 1939. If this October, 1939, curve of figure 3 be comparable with the October, 1938, curve of figure 1, it could be concluded that at Monterey in 1939 some pilchards entered the fall commercial fishery when in their second year. Nothing can be told by inspection of frequency curves in figures 1 and 3 about the ages of the fish larger than these sizes; they may be all one-year olds, or there may be an admixture of older fish. A knowledge of the age composition of these fish is possible only by determining the ages of the individual specimens.

The modes of curves in figure 1 do not coincide in position with analogous modes indicated for 1921 and 1922 (fig. 2). These differences may mean that the growth rate of the comparable year classes was different, or that survival was different; or it may mean that selection was different in 1938-39 than in 1921-22. In any event, it appears from these differences that one cannot generalize, as to size and growth, from one year class to another, or from the sampling of one year to that of another.

Young pilchards collected in Lower California in July and August, 1938, from Washington in April, September, and October, 1938, and from Oregon in May, 1939, do not correspond in size to those taken in California during those months. This indicates that the California bait fishery does not draw from the entire juvenile pilchard population of the Pacific coast. Lacking data for Lower California, Washington, and Oregon in other months, little can be judged from these data as to the age of fish represented in the available frequency curves. Are the fish taken in Lower California in July and August, 1938, fish in their first year, or their second? The same question may be asked about fish taken in Washington in April, September, and October, 1938, or at Coos Bay in May, 1939. These and other questions bearing on the age composition might be answered by study of the scales and otoliths.

AGE AND GROWTH OF JUVENILE PILCHARDS AS- JUDGED FROM SCALES AND OTOLITHS

The Use of Scales for Determining Age

The scales of pilchards are typical of fishes in the family Clupeidae. Like herring scales, they are sculptured on the upper surface of the unexposed part with low transverse folds, (Figure 12) which are in most specimens variously interrupted with rather coarse radii; and they are, with few exceptions, almost entirely unsculptured on their exposed part. Like herring scales, they differ from scales of many other species that are used for age determination, such as cod, haddock, or salmon, in that the surface folds--"circuli"--are typically not circular or concentric, but transect the scale from the dorsal to the ventral margins. Careful study has shown no irregularity in spacing between these folds, extending clear along their length, that can be related to age; there is no indication of winter narrowing of spaces, or of spring widening; nor any periodic change in texture that involves entire folds.

Close inspection of an adult pilchard scale, however, reveals other marks, concentric with the margin, along the line of which the transverse folds are more or less distorted and irregularly spaced. These are similar to the year marks on the scales of European herring, and are what Dr. Thompson counted as annuli in his study (1926) reviewed above, and also what the authors of this paper have considered as such.

If it could be demonstrated that they are really annual marks, the problem of determining the age of pilchards might then become a mere matter of counting them. However, they are not distinct in ordinary preparations, and special mounting is necessary to bring them out.

It was found during the present study that unless a pilchard scale be perfectly clean it is almost invariably useless ~~for~~ age determination. Because of the tenacity of the dried mucous, blood, guanin, etc., to the delicate surface structure, dirty pilchard scales cannot be cleaned, once they have dried, by washing in water and rubbing. Consequently, the scales must be cleaned at the time they are removed from the fish, before they are preserved in envelopes. For dirty, dried scales, a moderately satisfactory method of cleaning is the following: Soak the scale until thoroughly moistened in a 10 percent solution of sodium hydroxide, then rinse in water, rub with fingers to remove offal, rinse in 10 percent acetic acid to neutralize, and then rinse in clean water.

For mounting, many liquid media were tried: glycerine, water, mixtures of the two, and various kinds of oils and glues. These substances all rendered the scale too transparent for use, seriously decreasing the visibility of the surface structure, an effect found to be more or less proportional to the refractive index of the mounting medium (see figures 25 and 26).

It was found that pilchard scales appear to excellent advantage and the surface structure is brought out in bold relief in a medium of air. Accordingly, the specimens were mounted dry,--6 or 8 for each fish,-- between two glass slides stuck together at the ends with glue and clamped together tightly, until the latter dried, so as to flatten the scales and insure their remaining in place.^{2/} To mount scales from 100 fish required about 6 hours.

The specimens thus prepared were examined with the aid of a projecting microscope so arranged that the projected image appeared on the table beside the microscope. It is the impression of the authors, perhaps purely personal, but probably not, that the year marks appear much more clearly in the projected image than when viewed directly through the microscope.

For each specimen a punch card designed for the ready tabulating and sorting of data was laid on to the image so that a millimeter ruler printed on the card extended along the mid-longitudinal axis of the sculptured part of the scale, its zero line coinciding with the base of the latter. Lines were then drawn through the ruler where the latter was crossed by "annuli." Subsequently there were recorded on the card such pertinent data as sample number, length of fish, locality and date of collection, dimensions of scale and position of marks, etc. Thus a permanent quantitative record was obtained for every examination.

To learn the characteristics of an annual mark, scales of young pilchards were examined over the course of a year. A concentric mark was observed to have formed consistently by early spring. As a result of these preliminary examinations, we recognized as annuli those marks having the following characteristics:

An annulus is concentric with the margin of the scale. It is not always a sharp or unbroken line; nor are the segments of an interrupted annulus always perfectly cocircular (if the shape of a scale may be called circular in this discussion). But the course of an annulus, continuous or broken as it may be, can usually be traced, by careful scrutiny if necessary, entirely around the sculptured part of the scale from left-hand to right-hand margins. Sometimes they can even be followed around the unsculptured part. Annuli are clearly separated from each other and do not ordinarily meet at any point. If an annulus has formed, it is present in all the normal scales of an individual.

We have recognized as adventitious, or otherwise unperiodic ("false rings") those marks distinguished by the following characteristics:

^{2/}While this paper was in manuscript, a publication by Aikawa (1940) was received. It describes the same mounting technique as that used in our study.

They are merely short or unassociated arcs; or if they completely circle the sculptured part, they are usually not concentric with the margin; furthermore, they frequently join an annulus at the base. In any case, they may be less distinct than an annulus, being vague and indefinite, or they may be much more distinct, having a scarlike appearance; that is, with very pronounced irregularities of pattern, the folds being broken or otherwise obviously abnormal (See figures 24, 27). They rarely appear in all the scales of an individual

For the first annulus, which is sometimes difficult to distinguish from a scar, especially if it be nearer the center than normal, the following rule was applied: A mark conforming to the above description of an annulus was counted as an annulus, provided it appeared in all the scale specimens examined; but if in one or more specimens said mark had an obviously scarlike appearance, it was considered a false annulus, and was not counted.

Although a false annulus may appear at any time during the year, a true annulus is formed only once annually, and during a certain season. The distance between annulus and the margin of the scale--the marginal increment--represents the growth since the annulus was formed. For fish in their first year, the marginal increment is the distance between the base of the sculptured part and the margin of the scale. If one were choosing unperiodic marks to determine age in samples of fish, then frequency curves of the marginal increments should show no progress in width during the year, for there should be no consistency in the time of appearance or position of the marks. But, on the other hand, if one were choosing truly annual marks, there should be one time of year when the marginal increments are narrowest, and another time when they are widest, with intermediate widths between. This argument is the basis for the following test as to whether or not the annulus is formed once yearly.

A stratified random sample of 3,000 mounted scales was drawn (by Mosher) so as to represent about equally all the months of the period studied, and, where possible, to represent equally northern and southern California material. The labels of the slides were then masked, the slides mixed, and drawn at random from a box. The scales were then examined (by Malford), and measurements recorded as described above. Since the annulus is not apparent at the time it is forming on the very edge of the scale, but only sometime afterward when enough marginal growth has occurred to set it off clearly, no zero marginal increments were recorded. Figure 4 shows the marginal increments thus measured for scales with 0, 1, and 2 rings.

Obviously in the specimens of these year classes examined, the marginal increments were relatively narrow in April, 1938, and increased in width from then until the following fall, when narrow marginal increments began to appear again. In other words, the marks called annuli in this study must be really annual in occurrence, and may be used to determine age, at least for the first two years of life.

It has been argued (p. 5) from figure 1 that the group of small fish taken in June, 1938, with a dominant mode near 70 mm. represented fish spawned in 1938. According to the scale studies, the scales of these fish were consistently without annuli. It may therefore be supposed that fish with one and two rings on their scales at that time of year were of year classes 1937 and 1936, respectively. In November, one annulus became evident near the margin of some specimens identified from figure 1 as belonging to year class 1938. By March, all the members of this class had one annulus, while those having two and three were now identified with year classes 1937 and 1936, respectively.

If we choose an arbitrary boundary to separate "narrow" from "wide" marginal increments, say the 32.5 mm. point in the data used for figure 4, it is possible to define a time when the annulus became evident during 1938-39. The proportion of fish having "narrow" marginal increments, in percentage, by months, is given in figure 5. In southern California, according to figure 5, an annulus became evident, on the average, in pilchards of year classes 1937 and 1938 early in January, when 50 percent of the specimens examined showed a "narrow" marginal increment, and 50 percent a "wide" one. In central California the annulus did not appear until late February for year class 1938, early March for year class 1937.

This difference between central and southern California held consistently during the months for which comparable data are available (fig. 6). Since the scales were read without knowledge of the catch localities, this is further evidence that the marks called annuli had not been formed sporadically.

The annulus, being a very narrow zone, practically a line, became evident only when enough growth had occurred to expose it. Therefore it must have formed some time previous to the late fall and winter, probably in the late summer and fall, when, judging from figure 5, growth of the scales is slight.

If the evidence be accepted that the marks counted as annuli are really year marks, it remains to be shown whether the counts can be made with reasonable consistency. To test this, a stratified random sample of 242 scales that had already been read was drawn (by Mosher) from among some 3,000 scales, so as to represent with approximate equality the first four year classes. The labels of the slides were then masked, and the scales read for the second time (by Walford). The results, given in Table I, indicate that one person can count what he defines as year marks consistently.

To test the similarity of readings by two persons working separately, a sample of 367 scales from the fall fishery of 1939-40 that had been read by Walford was read independently by Mosher, with no previous experience at scale reading, and recorded as described on page 8. The results, given in table II, show a high percentage agreement between the two sets of readings, and indicate that at least two

persons can identify the same marks as annuli, and count the same number of rings in a significantly large proportion of the cases. The results summarized in both tables I and II give evidence that a year mark has been defined on page 8 in simple enough terms to serve as a usable guide. They do not necessarily indicate the percentage error in the counts of age rings, or in the relation between the number of rings present and the number of years of life, for it is well-nigh impracticable to obtain such a measure. For the present study, however, it is likely that this error is not disproportionately large; otherwise, figure 4 would have been a chaotic picture.

TABLE I.-Comparison of Original Scale Readings With Those Made at a Later Time by the Same Person.

Number of annuli in second reading	Number of first readings matching second	Number of first readings not matching second	Percentage agreement
0	64	0	100
1	50	4	93
2	70	3	96
3	<u>49</u>	<u>2</u>	96
	233	9	

TABLE II.-Comparison of Scale Readings by Two Different Persons

Number of annuli in second reading	Number of first readings matching second	Number of first readings not matching second	Percentage agreement
1	114	7	94
2	123	14	90
3	63	12	84
4	<u>30</u>	<u>4</u>	88
	330	37	

Although in this study the labels of the slides were masked, so as to obviate any possible bias caused by knowledge of the size of the fish, there was no way of concealing the size of the scales. The authors may thus have been influenced by scale size, tending to assign older ages to large scales and younger ages to smaller ones. If this influence were serious enough to dominate the determinations, the fact might become evident from a correlation study on age, body length, and scale length.

The latter two variables are rather imperfectly correlated, in the present material, with considerable variation of body length for each scale length, and also of scale length for each body length. (The coefficient of correlation between body length and scale length was .78, with P of less than .01. The coefficient of regression for scale length on body length was .84; that for body length on scale length was .73.) There is, of course, no way of knowing the true magnitude of correlation between age and either of these two variables. There are these possibilities for consideration, however:

(A.) Age might be more highly correlated with scale length than with body length. Then, on measuring scales from a number of fish with identical (or nearly so) body length, we should expect some degree of positive correlation between age and scale length. In addition, if, in our age determinations we had been influenced by the size of the scales, rather than the number of age marks, we should expect the above correlation to be enhanced. To examine this possibility, a collection of 987 scale measurements ranging from 190-219 mm. of projected image, and comprising four year classes, was divided into groups of ten-millimeter classes according to body length; and for each of these body-length classes the coefficient of correlation between age and scale length was calculated. The results, given in table III, show no significant correlation between these two quantities. The probability (P) is high, averaging .416, that if there were no correlation whatever, the coefficient could, by random causes alone, be as high as indicated. This lack of correlation is evidence that the age determinations were not influenced by scale length to any appreciable degree. Incidentally, it is also evidence that there is no intrinsic correlation between scale length and age; i.e., no correlation other than what results from the dependence of scale length on body length.

TABLE III.-Correlation (r) Between Age and Scale Length
for Fish of Identical Classes of Standard Length.

Body length of fish in millimeters date	N $\frac{1}{2}$	r	P
190-199 Nov. 1939	82	.21	> .05
190-199 Dec. 1939	91	.19	> .05
200-209 Nov. 1939	236	-.04	> .5
200-209 Dec. 1939	193	.002	> .9
210-219 Nov. 1939	174	.12	> .1
210-219 Dec. 1939	211	.003	> .9

$\frac{1}{2}$ Number of specimens

(B.) If, on the other hand, age is more highly correlated with body length than with scale length, we should expect some degree of positive correlation between age and body length among fish with identical (or nearly so) scale length. To examine this possibility, scales of 559 fish taken in the fall commercial fishery for adults, comprising four year classes, and ranging from 190-219 mm. in body length, were divided into 10 mm. classes according to scale length. The coefficient of correlation between body length and age within each of these scale-length classes was then calculated. These calculations (Table IV) show significant correlations between these two quantities, with a low probability (P), averaging less than one in one hundred, of arriving at such high values by chance alone, if there were no correlation. These results could not have been modified by any influence of scale length, for the design of the analysis precluded that.

TABLE IV.-Correlation (r) Between Age and Body Length for Fish Having Identical Scale Length Classification.

Scale length (mm. of projected image) Date	:	:	:	:	:
	:	N <u>1</u> /	:	r	:
	:		:		:
	:		:		:
190-199	:		:		:
Nov. 1939	:	55	:	.70	:
	:		:		:
190-199	:		:		:
Dec. 1939	:	50	:	.43	:
	:		:		:
200-209	:		:		:
Nov. 1939	:	81	:	.76	:
	:		:		:
200-209	:		:		:
Dec. 1939	:	84	:	.68	:
	:		:		:
210-219	:		:		:
Nov. 1939	:	152	:	.52	:
	:		:		:
210-219	:		:		:
Dec. 1939	:	137	:	.46	:
	:		:		:

1/ Number of specimens

(C.) The results reached under A and B are conclusive; but, nevertheless, consideration might be given to the possibility that age is correlated in like degree with both body length and scale length. Then the coefficient of correlation for age on body length with fish having identical (or nearly so) scale length, and that for age on scale length with fish having identical (or nearly so) body length should be about equal. Then, if in our age determination, the authors had been influenced by the size of the scales instead of the number of age marks, the correlation coefficient for age on body length should

tend to be the lower, and that for age on scale length the higher value of the two. Obviously, judging from tables III and IV, just the opposite of this result is demonstrated. Thus, so far as can be deduced from this evidence, there is no confirmation of a supposition that scale length significantly influenced the age determinations in the present study. Indeed, it appears unlikely that it was of any influence whatever.

The Use of Otoliths for Determining Age

Another line of evidence by which to judge the correctness of scale readings is given by a study of otoliths. This was carried on simultaneously by Mosher, independently of the scale work, and without reference to it.

Otoliths were collected from 6000 fish of the same series, described above, as represented by scales. These were washed and preserved in envelopes in the same manner as the scales. They were subsequently mounted as follows: A piece of thin cardboard was cut in the shape of a standard microscope slide, but about 1/8 of an inch shorter and narrower. This was punched with eight small round holes, and laid over a drop of Canada Balsam on a microscope slide. Into each hole was placed an otolith, then a drop of Canada balsam; and any air bubbles were burned out with a hot needle. Another microscope slide was laid on the mount as a cover glass, and the preparation put in a warm place to harden.

The mounted otoliths were examined in a micro-projection apparatus and the dimensions recorded on punch cards, as described on page 8, with the base of the ruler placed at the center, as indicated in Figure 28. The inner edge of each translucent zone was taken as representing the year mark. These readings were later checked by examination with a binocular microscope and reflected light, which brought out the year marks sharply as blue-black against the white opaque intervening zones.

Preliminary examination of otoliths from fish known to belong to 0 year class and collected over the course of 12 months established the following criteria of a year mark:

An annulus is a more or less translucent band concentric with the margin of the otolith, the intervening spaces being opaque. It can usually be traced entirely around the otolith, although it is more easily observed at the blunter anterior end than at the sides or posterior end. Annuli tend to be zones rather than lines.

Marks having the following characteristics were considered to be adventitious, or otherwise unperiodic:

Though translucent, they tend to be lines rather than zones; they frequently meet an annulus at some point.

Although the first two year-marks are generally well defined on otoliths, the third is less so; and the subsequent ones are so closely crowded and so easily confused with false year marks that they cannot be counted with a very high degree of confidence.

To determine whether or not the "annulus" is formed once annually in otoliths, a stratified random sample of 2600 specimens, representing about equally all the months of a year, was examined, and the marginal increments, which included the band comprising the annulus, were measured as described on page 8. To avoid possible confusion between true and false year marks in otoliths, no translucent zone was considered until it was wide enough to preclude its being a false annulus.

The marginal increments for otholiths, when plotted in the same way as had been done for scales in figure 4, proved also to be narrowest during one part of the year, and to increase progressively thereafter. In figure 7, age classes 1937, 1936, and 1938 have been assigned to fish having, at their first appearance in our samples, one, two, and zero rings on their otoliths, respectively. It is evident, in figure 7, that the annulus is a true year mark in otoliths as well as in scales, and became visible earlier in otoliths than in scales in 1939, showing as early as June in some specimens, and by October in all. This is consistent with the conclusion reached above that in scales the year mark forms during the summer and fall.

To define more exactly a time when the annulus became evident in otoliths, we can choose, from the data used for figure 7, arbitrary boundaries to separate "narrow" from "wide" marginal increments, as was done for scales. Thus the 35-mm. point was selected for year class 1938, the 20-mm. point for year class 1937, and the 15-mm. point for year class 1936. The proportion of fish having "narrow" marginal increments, in percentage, by months, is given in figure 8.

Parallel age determinations, by scales and by otoliths, were made in 1036 specimens. The results, given in table V. indicate a high agreement for the first two year classes, and a moderate agreement for the third. Doubtless a large portion of the disagreements among the three-year-olds may be attributed to the difficulty of counting the rings on otoliths with more than two marks.

Growth of Juvenile Pilchards

The age composition of samples from the 1938-39 bait fisheries of southern and central California, as determined by scales, is indicated in figure 9 where the growth of fish comprising year classes 1938 and

1937 can be traced from early youth to the size at entrance into the fall commercial fishery for adults; and though data for year class 1936, also included, are rather scanty, they are sufficient to give some indication of size composition and growth. A similar figure made from otolith readings was essentially identical with figure 9, and is therefore not here reproduced (Table 6).

TABLE V.- Comparison of Age Readings by Scales and by Otoliths

Number of annuli by scale reading	Number of otolith readings matching scale readings	Number of otolith readings not matching scale readings	Percentage agreement
1	355	6	98
2	419	36	92
3	<u>166</u>	<u>54</u>	75
	940	96	

Precise knowledge of the growth of the pilchard is seriously impeded by the difficulties of sampling, discussed on page 4. Growth is illustrated in figure 10 (Table 8) where the average lengths of each year class among fish taken in California are plotted by months. Data are from the bait fisheries and from the fall commercial fishery for adults.

The differences from year to year between the average length of fish of corresponding ages in figure 10 are no doubt due in part to actual differences between the year classes. In large part also, however, they are due to differential selection. Moreover, variations from a smooth growth curve for individual year classes are probably due to varying selection.

Samples of fish of year class 1937, taken from April, 1938, to May, 1939, were mostly from the southern California bait fisheries, where there is a tendency for bait fishermen to select against the larger fish, resulting in over-representation of the smaller members of that year class. Furthermore, judging from figure 9, there was a tendency for the larger fish of year class 1937 to leave, and for smaller ones to enter, the field of the fishery at intervals during the year. The consequent selective availability undoubtedly contributes to the irregularities of figure 10. From June to October, year class 1937, as well as 1936, was sampled from the San Francisco bait fisheries, which seemed to select against the smaller fish, producing an effect opposite to that obtained in southern California. At the same time, beginning in September, samples were taken from the fall fishery for adults at Monterey. Here a selection results from a rather complex differential availability. Fish of year class 1938 taken in the fall commercial fishery for adults appear to represent the larger members of their class, perhaps partly

because the latter were schooling with older fish, and partly because the fishermen consciously selected against very small fish, which have low economic value for reduction or canning purposes. In general the fish available during most of the fall are smaller and younger than those available during the winter. This results in a selection, by differential availability, against the larger fish of year classes 1937, 1936, and 1935.

Because of these differences in demand and availability from place to place, from fishery to fishery, and from month to month, and the consequent imperfections in our sampling of the population, figure 10 shows a very irregular series of points to which such a curve as might be fitted could only rather roughly represent the average growth of the pilchard in California during its first four years. Nevertheless, in all essential respects, the points, as far as they go, are in harmony with the points (designated by large asterisks) obtained from the modes of frequency curves in figure 2, and from data published by the California State Fisheries Laboratory (Clark, table 2, 1936).

Difference in Size Between Localities

The foregoing discussion has referred only to fish collected in California. The statistics given in figure 10 and table 8, therefore, describe only a portion of the total Pacific coast population of those year classes. That this is true is shown by figure 11, which gives the age composition of such samples as were obtainable in Washington, Oregon, and Lower California. Obviously, if it were possible to sample properly the entire coast, the range of each year class would probably be broader than shown in figure 9. Though the data from northern and southern grounds are too scanty to deserve very extensive interpretation, they show that fish found north of California in 1938-39 averaged smaller by the end of their first year than those of the same age from California; and fish taken from Lower California averaged larger than those of the same age taken in California. These differences are no doubt reflected in the scale growth increments, and should furnish a useful tool for studying migrations.

DISCUSSION AND CONCLUSIONS

The scales and otoliths of most fishes are characterized by folds or sculpturing in which variations of pattern may be related to age. If they are so related, for a given species, they need not correspond in number with years of life; or, if they do correspond, they may not be recognized, for they may be so obscure as to be counted incorrectly. It is no wonder, then, that scale and otolith reading is a process peculiarly open to subjective influences, and requires, for serious work, a stringent test and proof of validity.

In the foregoing pages it has been demonstrated that, if they be properly prepared, scales and otoliths of juvenile pilchards (Sardinops caerulea), show rings that are associated in number with age. It has been shown that these rings are formed once yearly, at a definite time of year, namely, the summer and fall. They therefore correspond in number with years of life. Though they are sometimes relatively obscure, the rings present may be counted with what appears to be significant accuracy, say 85-95 percent for the first three year classes; and results, which a later report will cover, give promise of extending the use of scales to much older ages. Of the scales examined during this study, over 99 percent were considered legible. Those not legible were generally specimens that had been improperly cleaned, or that had regenerated centers. The age determinations were in all cases made without reference to the size of the fish, and there is evidence that the operators were not unduly influenced by the size of the scales.

The counts of annuli on otoliths were found, by an independent study, to agree with those on scales. It is the opinion of the writers, however, that otoliths are less useful than scales for determining age of pilchards beyond the third year.

Judging from scales and otoliths of juvenile pilchards taken from the bait fisheries in California during 1938 and 1939, and from the fall commercial fishery for adults in 1939, fish of the year class 1938 had a modal length around 70 mm. when they first appeared in the bait fishery in June, 1938, growing to near 120 mm. by the following April, by which time the first annual mark has formed; and fish of year class 1937 had a modal length near 160 mm. when their second mark had formed. Because of the rather complex selection resulting from the requirements of the fisheries, as well as from variations in availability, the sampling was highly imperfect, and these figures are mere approximations. Furthermore, they apply only to fish taken from California fisheries.

Young specimens collected in Lower California were larger than those of corresponding age taken in California; and those taken in Oregon, Washington, and British Columbia were smaller. These differences suggest further applications of the study of pilchard scales, for they are, no doubt, reflected in differences in corresponding scale growth increments among the populations of the different regions. Thus the scales may prove useful for studying the migrations of the pilchard, as well as for determining their ages.

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TABLE VI -Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

MARCH, 1938		APRIL, 1938				May, 1938					
Fish length	Total fish measured	Fish aged				Total fish measured	Fish aged				Total fish measured
		From scales	From otoliths		From scales		From otoliths				
			Year classes				Year classes				
		37	36	37	36		37	36	37	36	
36	-	-	-	-	-	-	-	-	-	-	3
40	-	-	-	-	-	-	-	-	-	-	1
44	-	-	-	-	-	-	-	-	-	-	1
48	-	-	-	-	-	-	-	-	-	-	-
52	-	-	-	-	-	-	-	-	-	-	-
56	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	-	-	-	-
64	-	-	-	-	-	-	-	-	-	-	-
68	-	-	-	-	-	-	-	-	-	-	-
72	-	-	-	-	-	-	-	-	-	-	-
76	-	-	-	-	-	-	-	-	-	-	-
80	1	-	-	-	-	-	-	-	-	-	-
84	49	-	-	-	-	-	-	-	-	-	-
88	311	-	-	-	-	-	-	-	-	-	-
92	174	-	-	-	-	3	-	-	-	-	-
96	47	-	-	-	-	32	-	-	-	-	-
100	17	2	-	-	-	154	-	-	-	-	-
104	11	4	-	5	-	365	-	-	-	-	-
108	23	5	-	8	-	577	-	-	-	-	10
112	23	2	-	10	-	904	-	-	-	-	58
116	38	7	-	12	-	691	1	-	-	-	265
120	41	8	-	11	-	507	1	-	3	-	412
124	46	7	-	8	-	437	4	-	10	-	354
128	48	6	-	4	-	440	7	-	7	-	355
132	25	9	-	10	-	377	5	-	6	1	383
136	17	9	1	7	-	304	7	2	5	-	360
140	10	7	1	5	-	139	4	-	14	1	357
144	9	1	5	1	-	66	3	1	5	2	306
148	8	2	3	1	2	43	9	-	11	-	255
152	11	2	1	-	-	22	9	2	9	2	188
156	9	-	-	1	-	19	11	5	5	2	116
160	6	1	2	-	-	10	5	4	1	3	42
164	1	-	1	-	-	1	2	9	1	6	30
168	5	-	1	-	-	2	-	5	-	5	33
172	2	-	-	-	-	1	2	5	-	3	31
176	-	-	-	-	-	-	1	2	-	1	16
180	1	-	-	-	-	1	-	3	-	2	16
184	1	-	-	-	-	-	-	1	-	1	4
188	4	-	-	-	-	-	-	-	-	-	4
192	-	-	-	-	-	-	-	-	-	-	2
196	-	-	-	-	-	-	-	1	-	-	3
200	1	-	-	-	-	-	-	-	-	-	2
204	-	-	-	-	-	-	-	-	-	-	2
208	-	-	-	-	-	-	-	-	-	-	-
212	-	-	-	-	-	1	-	-	-	-	1
216	-	-	-	-	-	-	-	-	-	-	-
220	-	-	-	-	-	-	-	-	-	-	1
224	-	-	-	-	-	-	-	-	-	-	1
228	-	-	-	-	-	-	-	-	-	-	-
232	-	-	-	-	-	-	-	-	-	-	-
236	-	-	-	-	-	-	-	-	-	-	-
240	-	-	-	-	-	-	-	-	-	-	-
244	-	-	-	-	-	-	-	-	-	-	-
248	-	-	-	-	-	-	-	-	-	-	-
252	-	-	-	-	-	-	-	-	-	-	-
256	-	-	-	-	-	-	-	-	-	-	1
TOTALS	939	72	15	83	2	5096	71	40	77	29	3614

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

Fish length	JUNE, 1938						JULY, 1938						Total fish measured	
	Fish aged From scales			From otoliths			Fish aged From scales			From otoliths				
	Year classes						Year classes							
	38	37	36	38	37	36	38	37	36	38	37	36		
36	-	-	-	-	-	-	-	-	-	-	-	-	-	
40	-	-	-	1	-	-	-	-	-	-	-	-	-	
44	-	-	-	3	-	-	65	-	-	-	-	-	-	
48	-	-	-	3	-	-	31	-	-	-	-	-	-	
52	-	-	-	1	-	-	10	-	-	-	-	-	-	
56	-	-	-	2	-	-	17	-	-	-	-	-	5	
60	1	-	-	3	-	-	28	2	-	-	1	-	24	
64	2	-	-	6	-	-	38	4	-	-	4	-	103	
68	2	-	-	9	-	-	36	4	-	-	6	-	156	
72	1	-	-	9	-	-	27	4	-	-	6	-	151	
76	-	-	-	10	-	-	31	7	-	-	7	-	141	
80	-	-	-	7	-	-	103	9	-	-	12	-	184	
84	-	-	-	4	-	-	92	4	-	-	14	-	134	
88	-	-	-	5	-	-	29	5	-	-	17	-	156	
92	-	-	-	3	-	-	5	1	-	-	8	-	105	
96	-	-	-	2	-	-	2	1	-	-	5	-	64	
100	-	-	-	-	-	-	2	2	-	-	1	-	35	
104	-	-	-	2	-	-	1	-	-	-	1	-	11	
108	-	-	-	-	-	-	-	1	-	-	-	-	3	
112	-	-	-	-	-	-	-	-	-	-	1	-	8	
116	-	1	-	-	-	-	1	-	-	-	1	-	2	
120	-	-	-	-	4	-	14	-	-	-	-	-	5	
124	-	2	-	-	5	-	72	-	-	-	-	-	7	
128	-	9	-	-	7	-	272	-	-	-	-	-	47	
132	-	10	-	-	11	-	556	-	2	-	-	-	197	
136	-	8	-	-	10	-	778	-	4	-	4	-	337	
140	-	12	-	-	11	-	791	-	2	-	5	-	578	
144	-	10	-	-	8	1	651	-	15	1	12	-	517	
148	-	10	-	-	4	-	477	-	6	-	10	-	403	
152	-	12	1	-	4	2	362	-	11	-	6	-	270	
156	-	15	6	-	3	3	240	-	6	-	-	-	216	
160	-	12	4	-	1	1	180	-	8	1	4	2	149	
164	-	6	12	-	-	3	87	-	9	-	4	4	111	
168	-	-	11	-	-	-	46	-	6	2	-	2	64	
172	-	1	11	-	-	-	28	-	1	3	-	3	31	
176	-	-	6	-	-	-	16	-	1	4	-	3	30	
180	-	-	5	-	-	1	11	-	-	-	-	1	14	
184	-	-	4	-	-	1	8	-	-	1	-	1	11	
188	-	-	1	-	-	-	3	-	-	-	-	1	8	
192	-	-	1	-	-	-	3	-	-	-	-	1	2	
196	-	-	-	-	-	-	2	-	-	1	-	1	5	
200	-	-	-	-	-	-	2	-	-	1	-	2	1	
204	-	-	-	-	-	-	2	-	-	-	-	-	3	
208	-	-	-	-	-	-	3	-	-	-	-	-	2	
212	-	-	-	-	-	-	3	-	-	-	-	-	2	
216	-	-	-	-	-	-	3	-	-	-	-	-	1	
220	-	-	-	-	-	-	1	-	-	-	-	-	-	
224	-	-	-	-	-	-	1	-	-	-	-	-	-	
228	-	-	-	-	-	-	1	-	-	-	-	-	-	
232	-	-	-	-	-	-	-	-	-	-	-	-	-	
236	-	-	-	-	-	-	2	-	-	-	-	-	-	
240	-	-	-	-	-	-	-	-	-	-	-	-	-	
244	-	-	-	-	-	-	-	-	-	-	-	-	-	
248	-	-	-	-	-	-	1	-	-	-	-	-	-	
252	-	-	-	-	-	-	1	-	-	-	-	-	-	
256	-	-	-	-	-	-	-	-	-	-	-	-	-	
TOTALS	6	108	65	70	68	12	5141	44	70	14	84	52	21	4293

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

AUGUST, 1938							SEPTEMBER, 1938							
Fish length	Fish aged						Total fish measured	Fish aged						Total fish measured
	From scales			From otoliths				From scales			From otoliths			
	Year classes							Year classes						
	38	37	36	38	37	36		38	37	36	38	37	36	
52	1	-	-	-	-	-	1	-	-	-	-	-	-	-
56	-	-	-	-	-	-	1	-	-	-	-	-	-	-
60	1	-	-	-	-	-	5	-	-	-	-	-	-	-
64	4	-	-	4	-	-	47	-	-	-	-	-	-	-
68	7	-	-	6	-	-	202	-	-	-	1	-	-	16
72	19	-	-	16	-	-	304	-	-	-	2	-	-	75
76	14	-	-	29	-	-	284	3	-	-	5	-	-	242
80	10	-	-	20	-	-	118	5	-	-	12	-	-	287
84	3	-	-	2	-	-	34	10	-	-	13	-	-	242
88	3	-	-	1	-	-	10	8	-	-	10	-	-	187
92	3	-	-	-	-	-	9	11	-	-	14	-	-	210
96	1	-	-	1	-	-	8	5	-	-	14	-	-	211
100	6	-	-	-	-	-	7	14	-	-	15	-	-	76
104	1	-	-	1	-	-	9	7	-	-	7	-	-	18
108	-	-	-	-	-	-	1	1	-	-	2	-	-	5
112	1	-	-	-	-	-	3	-	-	-	-	-	-	3
116	-	1	-	-	-	-	2	-	-	-	-	-	-	4
120	-	-	-	-	-	-	2	1	-	-	1	-	-	2
124	-	-	-	-	-	-	3	-	-	-	-	-	-	4
128	-	2	-	-	-	-	9	-	-	-	-	-	-	24
132	-	6	-	-	1	-	67	-	-	-	-	-	-	104
136	-	16	-	-	7	-	238	-	2	-	-	1	-	288
140	-	24	1	-	13	-	476	-	4	-	-	6	-	489
144	-	23	2	-	20	-	630	-	9	-	-	10	-	686
148	-	25	-	-	18	-	678	-	14	1	-	13	-	671
152	-	11	3	-	16	1	549	-	16	2	-	19	-	517
156	-	10	-	-	14	1	351	-	7	1	-	14	-	327
160	-	5	-	-	10	2	174	-	6	-	-	11	-	175
164	-	2	1	-	2	1	107	-	-	-	-	3	-	74
168	-	3	-	-	1	1	70	-	-	-	-	1	2	91
172	-	1	1	-	1	1	49	-	-	3	-	1	2	68
176	-	1	1	-	-	2	50	-	-	-	-	-	-	59
180	-	-	2	-	-	1	47	-	-	-	-	-	-	49
184	-	-	2	-	-	2	33	-	-	-	-	-	-	19
188	-	-	-	-	-	1	28	-	-	-	-	-	-	16
192	-	-	1	-	-	-	29	-	-	-	-	-	-	8
196	-	-	-	-	-	1	10	-	-	-	-	-	-	2
200	-	-	-	-	-	1	11	-	-	-	-	-	-	1
204	-	-	-	-	-	-	18	-	-	-	-	-	-	2
208	-	-	-	-	-	-	5	-	-	-	-	-	-	1
212	-	-	-	-	-	-	11	-	-	-	-	-	-	1
216	-	-	-	-	-	-	7	-	-	-	-	-	-	1
220	-	-	-	-	-	-	3	-	-	-	-	-	-	-
224	-	-	-	-	-	-	2	-	-	-	-	-	-	-
228	-	-	-	-	-	-	-	-	-	-	-	-	-	1
232	-	-	-	-	-	-	-	-	-	-	-	-	-	1
236	-	-	-	-	-	-	1	-	-	-	-	-	-	-
TOTALS	74	129	14	80	103	15	4703	65	58	7	96	79	4	5257

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

Fish length	OCTOBER, 1938						Total fish measured	NOVEMBER, 1938						Total fish measured
	Fish aged			From otoliths	Fish aged			From otoliths						
	From scales	Year classes			From scales	Year classes								
		38	37			36			38	37	36			
60	-	-	-	-	-	-	1	-	-	-	-	-	-	-
64	-	-	-	-	-	-	14	-	-	-	-	-	-	-
68	-	-	-	-	-	-	34	-	-	-	-	-	-	-
72	-	-	-	-	-	-	17	-	-	-	-	-	-	-
76	1	-	-	2	-	-	55	-	-	-	-	-	-	-
80	8	-	-	5	-	-	212	-	-	-	-	-	-	13
84	14	-	-	5	-	-	350	2	-	-	3	-	-	40
88	13	-	-	9	-	-	262	3	-	-	4	-	-	112
92	5	-	-	6	-	-	222	5	-	-	9	-	-	180
96	1	-	-	7	-	-	344	5	-	-	9	-	-	262
100	2	-	-	6	-	-	277	1	-	-	4	-	-	154
104	7	-	-	5	-	-	202	-	-	-	3	-	-	111
108	5	-	-	6	-	-	95	2	-	-	2	-	-	143
112	3	-	-	-	-	-	85	4	-	-	3	-	-	127
116	2	-	-	1	-	-	94	5	-	-	4	-	-	107
120	3	-	-	2	-	-	95	5	-	-	5	-	-	55
124	2	-	-	-	-	-	72	6	1	-	5	-	-	37
128	2	1	-	1	-	-	62	-	-	-	-	-	-	31
132	-	1	-	-	-	-	55	1	1	-	2	-	-	24
136	-	3	-	-	-	-	166	1	-	-	-	-	-	16
140	1	10	-	-	1	-	363	1	-	-	-	-	-	22
144	-	4	-	-	2	-	494	-	2	-	-	-	-	78
148	-	11	-	-	4	-	469	-	6	-	-	-	-	198
152	-	22	1	1	17	-	473	1	7	-	-	2	-	416
156	-	19	1	-	22	-	390	-	8	1	-	-	-	760
160	-	16	3	-	20	1	218	-	6	-	-	13	-	800
164	-	6	1	-	12	1	125	-	11	-	-	13	-	670
168	-	3	1	-	3	1	65	-	8	1	-	13	1	548
172	-	1	3	-	2	-	37	-	2	1	-	8	-	480
176	-	1	1	-	1	-	55	-	7	5	-	5	6	397
180	-	-	-	-	1	-	80	-	2	4	-	3	4	283
184	-	-	-	-	-	2	81	-	2	4	-	-	7	211
188	-	-	-	-	1	2	86	-	-	6	-	-	6	147
192	-	-	-	-	-	2	70	-	-	3	-	-	2	82
196	-	-	-	-	-	4	50	-	-	3	-	-	2	64
200	-	-	-	-	-	2	35	-	-	2	-	-	1	59
204	-	-	-	-	-	1	20	-	-	1	-	-	2	46
208	-	-	-	-	-	-	17	-	-	1	-	-	-	38
212	-	-	-	-	-	-	6	-	-	-	-	-	-	32
216	-	-	-	-	-	-	6	-	-	1	-	-	-	35
220	-	-	-	-	-	-	6	-	-	2	-	-	-	16
224	-	-	-	-	-	-	-	-	-	-	-	-	-	8
228	-	-	-	-	-	-	-	-	-	-	-	-	-	2
232	-	-	-	-	-	-	1	-	-	-	-	-	-	2
236	-	-	-	-	-	-	1	-	-	-	-	-	-	2
240	-	-	-	-	-	-	-	-	-	-	-	-	-	1
244	-	-	-	-	-	-	-	-	-	-	-	-	-	1
248	-	-	-	-	-	-	-	-	-	-	-	-	-	1
252	-	-	-	-	-	-	-	-	-	-	-	-	-	-
256	-	-	-	-	-	-	-	-	-	-	-	-	-	1
260	-	-	-	-	-	-	-	-	-	-	-	-	-	-
264	-	-	-	-	-	-	-	-	-	-	-	-	-	1
TOTALS	69	98	11	56	86	16	5862	42	63	35	53	57	31	6812

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

DECEMBER, 1938								JANUARY, 1939							
Fish length	Fish aged						Total fish measured	Fish aged						Total fish measured	
	From scales			From otoliths				From scales			From otoliths				
	Year classes							Year classes							
	38	37	36	38	37	36		38	37	36	38	37	36		
68	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
72	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
76	-	-	-	-	-	-	-	-	-	-	-	-	-	1	
80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
84	-	-	-	-	-	-	3	1	-	-	-	-	-	6	
88	-	-	-	-	-	-	27	4	-	-	1	-	-	34	
92	4	-	-	2	-	-	115	6	-	-	2	-	-	121	
96	17	-	-	6	-	-	200	5	-	-	3	-	-	155	
100	16	-	-	5	-	-	166	3	-	-	6	-	-	129	
104	4	-	-	1	-	-	113	2	-	-	10	-	-	164	
108	4	-	-	-	-	-	114	3	-	-	9	-	-	158	
112	3	-	-	2	-	-	104	7	-	-	1	-	-	199	
116	-	-	-	5	-	-	89	7	-	-	4	-	-	333	
120	1	-	-	1	-	-	75	8	-	-	9	-	-	390	
124	1	-	-	6	-	-	53	4	-	-	2	-	-	273	
128	-	-	-	2	-	-	33	2	1	-	2	-	-	160	
132	-	-	-	-	-	-	19	-	-	-	1	-	-	81	
136	-	-	-	-	-	-	14	4	-	-	-	-	-	53	
140	-	-	-	1	-	-	17	-	1	-	-	1	-	39	
144	-	-	-	-	1	-	30	1	1	-	-	1	-	96	
148	-	1	-	-	-	-	65	-	3	-	-	2	-	187	
152	-	3	-	-	3	-	148	1	19	-	-	2	-	350	
156	-	5	-	-	4	-	328	-	19	2	-	7	-	550	
160	-	11	-	-	16	-	438	-	28	-	-	10	1	684	
164	-	6	3	-	8	1	490	-	18	1	-	11	-	639	
168	-	6	2	-	12	-	394	-	2	1	-	13	7	392	
172	-	9	2	-	14	4	346	-	3	-	-	10	3	230	
176	-	8	8	-	5	8	247	-	-	-	-	6	1	129	
180	-	8	7	-	3	5	157	-	-	2	-	-	4	88	
184	-	3	1	-	3	1	114	-	-	1	-	-	4	67	
188	-	1	2	-	-	2	96	-	3	1	-	1	1	72	
192	-	1	1	-	-	1	93	-	-	1	-	-	4	64	
196	-	-	1	-	-	-	77	-	1	2	-	-	-	44	
200	-	-	1	-	-	-	61	-	-	-	-	-	-	33	
204	-	-	-	-	-	-	48	-	-	2	-	-	1	28	
208	-	-	-	-	-	-	46	-	-	-	-	-	-	21	
212	-	-	-	-	-	-	36	-	-	-	-	-	-	10	
216	-	-	-	-	-	-	22	-	-	-	-	-	-	14	
220	-	-	-	-	-	-	8	-	-	-	-	-	-	6	
224	-	-	-	-	-	-	15	-	-	-	-	-	-	7	
228	-	-	-	-	-	-	6	-	-	-	-	-	-	6	
232	-	-	-	-	-	-	5	-	-	-	-	-	-	2	
236	-	-	-	-	-	-	3	-	-	-	-	-	-	1	
240	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
244	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
248	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
252	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
256	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
260	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
264	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
268	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
272	-	-	-	-	-	-	1	-	-	-	-	-	-	-	
TOTALS	50	62	28	31	69	22	4418	59	99	13	50	64	26	6017	

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

	FEBRUARY, 1939							MARCH, 1939						
Fish length	Fish aged From scales			From otoliths			Total fish measured	Fish aged From scales			From otoliths			Total fish measured
	Year classes							Year classes						
	38	37	36	38	37	36		38	37	36	38	37	36	
76	-	-	-	-	-	-	1	-	-	-	-	-	-	-
90	-	-	-	-	-	-	7	-	-	-	-	-	-	7
81	-	-	-	-	-	-	7	1	-	-	1	-	-	39
92	1	-	-	1	-	-	16	4	-	-	4	-	-	103
96	3	-	-	4	-	-	96	4	-	-	5	-	-	244
96	19	-	-	18	-	-	279	7	-	-	6	-	-	496
100	11	-	-	13	-	-	354	2	-	-	7	-	-	611
104	5	-	-	2	-	-	209	2	-	-	4	-	-	427
108	6	-	-	1	-	-	125	6	-	-	5	-	-	427
112	4	-	-	-	-	-	70	9	-	-	9	-	-	546
116	-	-	-	-	-	-	63	12	-	-	4	-	-	574
120	5	-	-	4	-	-	80	29	-	-	15	-	-	575
124	5	-	-	3	-	-	66	32	-	-	12	-	-	539
128	6	-	-	3	-	-	62	22	-	-	7	-	-	496
132	3	1	-	-	-	-	86	9	-	-	6	-	-	340
136	1	-	-	1	1	-	89	5	-	-	5	-	-	271
140	3	4	-	3	3	-	105	7	-	-	7	1	-	201
144	3	2	-	-	2	-	109	1	-	-	4	1	-	184
148	-	8	1	-	4	-	108	-	2	-	9	-	-	125
152	1	10	-	-	6	-	136	-	1	-	5	-	-	76
156	-	12	-	1	8	-	213	-	1	-	2	1	-	49
160	-	21	1	-	10	-	282	-	3	-	-	1	-	50
164	-	17	4	-	8	-	236	-	7	1	-	1	-	69
168	-	19	3	-	3	-	132	-	13	1	-	3	1	129
172	-	12	3	-	2	-	96	-	27	5	-	7	-	179
176	-	8	2	-	-	-	93	-	35	4	-	5	2	223
180	-	7	5	-	1	-	122	-	40	11	-	12	7	246
184	-	9	3	-	1	2	136	-	29	12	-	4	14	228
188	-	1	2	-	-	4	117	-	15	18	-	5	11	170
192	-	1	6	-	-	4	106	-	4	12	-	-	10	95
196	-	-	1	-	-	4	86	-	3	8	-	-	6	68
200	-	-	2	-	-	2	51	-	-	8	-	-	4	35
204	-	-	-	-	-	1	35	-	-	5	-	-	2	17
208	-	-	-	-	-	2	30	-	-	1	-	-	2	6
212	-	-	-	-	-	-	18	-	-	-	-	-	-	2
216	-	-	-	-	-	1	15	-	-	-	-	-	-	1
220	-	-	-	-	-	-	6	-	-	-	-	-	-	-
224	-	-	-	-	-	-	3	-	-	-	-	-	-	-
228	-	-	-	-	-	-	3	-	-	-	-	-	-	-
232	-	-	-	-	-	-	-	-	-	-	-	-	-	-
236	-	-	-	-	-	-	-	-	-	-	-	-	-	-
240	-	-	-	-	-	-	1	-	-	-	-	-	-	-
244	-	-	-	-	-	-	-	-	-	-	-	-	-	-
248	-	-	-	-	-	-	1	-	-	-	-	-	-	-
252	-	-	-	-	-	-	-	-	-	-	-	-	-	1
256	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTALS	76	132	33	54	49	20	3850	152	180	86	117	41	59	7879

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

Fish length	APRIL, 1939						MAY, 1939						
	Fish aged			Total fish measured	Fish aged			Total fish measured					
	From scales	From otoliths			From scales	From otoliths							
		Year classes				Year classes							
	38	37	36	38	37	36	38	37	36	38	37	36	
92	-	-	-	-	-	-	-	-	-	-	-	-	
96	1	-	-	-	-	-	-	-	-	-	-	-	
100	1	-	-	-	-	-	-	-	-	-	-	-	
104	4	-	-	-	-	-	-	-	-	-	-	2	
108	8	-	-	8	-	-	-	-	-	-	-	14	
112	19	-	-	12	-	-	-	-	-	-	-	32	
116	32	-	-	11	-	-	1	-	-	-	-	81	
120	26	-	-	12	-	-	10	-	-	6	-	168	
124	36	-	-	16	-	-	28	-	-	13	-	277	
128	24	-	-	8	-	-	19	-	-	7	-	233	
132	16	-	-	6	-	-	7	-	-	2	-	177	
136	11	1	-	3	-	-	3	-	-	-	-	111	
140	13	1	-	4	-	-	1	-	-	1	-	62	
144	6	-	-	1	-	-	-	-	-	-	-	39	
148	2	1	-	-	-	-	-	-	-	-	-	29	
152	1	2	-	1	2	-	-	-	-	-	-	22	
156	1	5	-	1	1	-	4	2	-	2	2	33	
160	-	6	-	-	6	-	-	2	-	-	-	34	
164	-	13	1	-	2	1	1	1	1	2	-	34	
168	-	18	-	-	8	-	-	4	1	1	-	40	
172	-	23	-	-	9	-	-	11	2	-	10	54	
176	-	12	3	-	18	2	-	7	-	-	7	61	
180	-	14	3	-	5	-	-	11	2	-	15	104	
184	-	9	1	-	4	-	-	20	2	-	18	179	
188	-	1	-	-	-	-	-	14	2	-	7	115	
192	-	1	-	-	-	-	-	12	3	-	9	99	
196	-	1	-	-	-	-	-	6	2	-	4	51	
200	-	1	1	-	-	-	-	1	1	-	2	3	
204	-	-	-	-	-	-	-	2	6	-	-	3	
208	-	-	-	-	-	-	-	1	2	-	1	2	
212	-	-	-	-	-	1	-	-	3	-	-	1	
216	-	-	-	-	-	-	-	-	3	-	-	1	
220	-	-	-	-	-	-	-	-	-	-	-	-	
224	-	-	-	-	-	-	-	1	-	-	-	2	
228	-	-	-	-	-	-	-	-	-	-	-	-	
232	-	-	-	-	-	-	-	-	-	-	-	-	
236	-	-	-	-	-	-	-	-	-	-	-	-	
240	-	-	-	-	-	-	-	-	-	-	-	-	
244	-	-	-	-	-	-	-	-	-	-	-	1	
248	-	-	-	-	-	-	-	-	-	-	-	-	
252	-	-	-	-	-	-	-	-	-	-	-	-	
256	-	-	-	-	-	-	-	-	-	-	-	-	
TOTALS	201	108	9	83	55	4	77	95	30	35	76	35	2106

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

Fish length	JUNE, 1939						Total fish measured	JULY, 1939						Total fish measured
	Fish aged			From otoliths	Total fish measured	Fish aged			From otoliths	Total fish measured				
	From scales	Year classes				From scales		Year classes						
	38	37	36			38		37			36	38	37	
124	-	-	-	-	-	-	1	-	-	-	-	-	-	-
128	1	-	-	1	-	-	17	-	-	-	-	-	-	-
132	2	-	-	1	-	-	48	-	-	-	-	-	-	-
136	5	-	-	3	-	-	114	-	-	-	-	-	-	-
140	9	-	-	5	-	-	92	-	-	-	-	-	-	-
144	8	-	-	4	-	-	103	-	-	-	-	-	-	-
148	4	-	-	-	-	-	83	-	-	-	-	-	-	-
152	3	-	-	-	-	-	33	-	-	-	-	-	-	1
156	3	-	-	1	-	-	51	-	-	-	-	-	-	2
160	9	-	-	2	-	-	26	-	-	-	1	-	-	1
164	1	1	-	-	-	1	11	-	-	-	-	-	-	-
168	1	-	-	-	-	-	12	-	-	-	-	-	-	1
172	-	3	-	-	1	1	14	-	1	-	1	-	-	6
176	-	6	-	-	4	-	25	1	3	-	1	-	-	3
180	-	3	-	-	1	-	24	-	1	-	-	-	-	2
184	-	7	1	-	5	3	24	-	2	-	-	-	-	15
188	-	2	1	-	2	2	22	-	12	2	-	5	-	14
192	-	4	2	-	4	3	22	-	10	3	-	3	-	35
196	-	3	4	-	5	2	16	-	21	4	-	5	4	49
200	-	4	4	-	7	2	17	-	12	11	-	7	3	59
204	-	4	2	-	2	5	6	-	12	23	-	14	11	54
208	-	3	5	-	3	5	10	-	5	20	-	4	18	48
212	-	-	9	-	-	10	6	-	3	14	-	-	11	21
216	-	-	-	-	-	-	3	-	-	8	-	-	7	16
220	-	-	2	-	-	2	-	-	-	2	-	-	2	10
224	-	-	-	-	-	-	-	-	-	1	-	-	-	5
228	-	-	-	-	-	-	-	-	-	-	-	-	-	1
232	-	-	-	-	-	-	-	-	-	-	-	-	-	2
236	-	-	-	-	-	-	-	-	-	-	-	-	-	1
240	-	-	-	-	-	-	-	-	-	-	-	-	-	1
244	-	-	-	-	-	-	-	-	-	-	-	-	-	2
248	-	-	-	-	-	-	-	-	-	-	-	-	-	1
252	-	-	-	-	-	-	-	-	-	-	-	-	-	1
256	-	-	-	-	-	-	-	-	-	-	-	-	-	3
260	-	-	-	-	-	-	-	-	-	-	-	-	-	1
TOTALS	46	40	30	17	34	36	780	1	82	88	-	41	56	355

TABLE VI (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled in California, by Ages.

	AUGUST, 1939						SEPTEMBER, 1939							
Fish length	Fish aged			From			Total fish measured	Fish aged			From			Total fish measured
	From scales			otoliths				From scales			otoliths			
	38	37	36	38	37	36		38	37	36	38	37	36	
156	-	-	-	-	-	-	-	-	-	-	-	-	-	5
160	-	-	-	-	-	-	-	-	-	-	-	-	-	3
164	-	-	-	-	-	-	-	-	-	-	-	-	-	5
168	3	-	-	5	-	-	6	-	1	-	-	-	-	10
172	1	-	-	1	1	-	5	-	1	-	-	-	-	15
176	6	1	-	5	2	-	11	-	1	-	-	-	-	7
180	3	1	-	5	4	1	13	-	2	-	-	-	-	7
184	-	3	-	1	2	-	7	-	1	-	-	-	-	8
188	-	1	-	-	3	-	14	-	1	-	-	-	-	5
192	-	9	3	-	6	1	38	-	3	1	-	-	-	19
196	1	14	1	-	7	3	56	-	6	2	-	-	-	40
200	-	16	12	-	4	9	82	-	18	5	-	-	-	59
204	-	38	29	-	9	13	75	-	27	36	-	-	-	78
208	-	36	51	-	3	15	100	-	17	27	-	-	-	60
212	-	24	56	-	4	14	75	-	10	19	-	-	-	36
216	-	5	41	-	-	9	43	-	-	11	-	-	-	13
220	-	1	21	-	-	4	27	-	1	3	-	-	-	6
224	-	-	6	-	-	1	6	-	1	-	-	-	-	2
228	-	-	1	-	-	-	3	-	-	-	-	-	-	1
232	-	-	-	-	-	-	1	-	-	-	-	-	-	-
236	-	-	-	-	-	-	1	-	-	-	-	-	-	-
240	-	-	-	-	-	-	-	-	-	-	-	-	-	-
244	-	-	-	-	-	-	1	-	-	-	-	-	-	-
248	-	-	-	-	-	-	-	-	-	-	-	-	-	-
252	-	-	-	-	-	-	-	-	-	-	-	-	-	-
256	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTALS	14	149	221	17	45	70	567	-	90	104	-	-	-	379

OCTOBER, 1939							
Fish length	Fish aged			From			Total fish measured
	From scales	Year classes			From otoliths		
		38	37	36			
	38	37	36	38	37	36	
172	-	-	-	-	-	-	3
176	-	-	-	-	-	-	2
180	-	-	-	-	-	-	5
184	-	-	-	-	-	-	3
188	-	-	-	-	-	-	8
192	-	-	-	-	-	-	4
196	-	-	-	-	-	-	25
200	-	8	2	-	-	-	38
204	-	23	9	-	-	-	51
208	-	4	9	-	-	-	23
212	-	4	7	-	-	-	19
216	-	4	3	-	-	-	13
220	-	-	4	-	-	-	4
TOTALS	-	43	34	-	-	-	198

TABLE VII.-Frequency Record of Juvenile Pilchards Sampled Outside California,
by Ports and by Ages.

JULY, 1938							AUGUST, 1938							
Southern Lower California							Central Lower California							
Fish length	Fish aged			From			Total fish measured	Fish aged			From			Total fish measured
	From scales			otoliths				From scales			otoliths			
	Year classes							Year classes						
	38	37	36	38	37	36		38	37	36	38	37	36	
64	-	-	-	-	-	-	-	1	-	-	-	-	-	1
68	-	-	-	-	-	-	1	2	-	-	1	-	-	10
72	-	-	-	-	-	-	25	3	-	-	4	-	-	15
76	-	-	-	-	-	-	68	2	-	-	10	-	-	55
80	-	-	-	1	-	-	271	7	-	-	4	-	-	41
84	-	-	-	5	-	-	404	6	-	-	8	-	-	32
88	1	-	-	8	-	-	244	5	-	-	1	-	-	10
92	1	-	-	4	-	-	140	1	-	-	-	-	-	3
96	3	-	-	1	-	-	84	-	-	-	1	-	-	4
100	4	-	-	1	-	-	57	4	-	-	4	-	-	14
104	3	-	-	4	-	-	58	5	-	-	8	-	-	28
108	5	-	-	7	-	-	63	7	-	-	11	-	-	26
112	10	-	-	7	-	-	77	6	-	-	6	-	-	14
116	11	-	-	6	-	-	73	3	-	-	2	-	-	8
120	10	-	-	1	-	-	62	1	1	-	2	-	-	3
124	9	1	-	1	-	-	35	-	-	-	-	-	-	-
128	2	-	-	-	-	-	20	-	-	-	-	-	-	-
132	3	-	-	-	-	-	8	-	-	-	-	-	-	-
136	-	-	-	-	-	-	2	-	-	-	-	-	-	-
140	-	-	-	-	-	-	2	-	-	-	-	-	-	-
144	-	-	-	-	-	-	-	-	-	-	-	-	-	-
148	-	-	-	-	-	-	-	-	-	-	-	-	-	-
152	-	-	-	-	-	-	-	-	-	-	-	-	-	-
156	-	-	-	-	-	-	-	-	-	-	-	-	-	-
160	-	-	-	-	-	-	-	-	-	-	-	-	-	-
164	-	-	-	-	-	-	-	-	-	-	-	-	-	-
168	-	-	-	-	-	-	-	-	-	-	-	-	-	-
172	-	-	-	-	-	-	-	-	-	-	-	-	-	-
176	-	-	-	-	-	1	-	-	-	-	-	-	-	-
180	-	-	-	-	-	-	-	-	-	-	-	-	-	-
184	-	-	-	-	-	-	-	-	-	-	-	-	-	-
188	-	-	-	-	-	-	-	-	-	-	-	-	-	-
192	-	-	-	-	-	-	-	-	-	-	-	-	-	-
196	-	-	1	-	-	-	-	-	-	-	-	-	-	-
TOTALS	62	1	1	46	-	1	1694	53	1	-	62	-	-	264

TABLE VII (Cont'd.).-Frequency Record of Juvenile Pilchards Sampled Offshore California, by Ports and by Ages.

SEPTEMBER, 1938								OCTOBER, 1938							
Washington								Washington							
Fish length	From scales	Fish aged			From otoliths	Total fish measured		From scales	Fish aged			From otoliths	Total fish measured		
		Year classes							Year classes						
		38	37	36					38	37	36				38
60	-	-	-	-	-	-	5	-	-	-	-	-	7		
64	-	-	-	-	-	-	8	-	-	-	-	-	5		
68	-	-	-	-	-	-	9	-	-	-	-	-	11		
72	-	-	-	-	-	-	4	-	-	-	-	-	6		
76	-	-	-	-	-	-	-	-	-	-	-	-	4		
80	-	-	-	-	-	-	-	-	-	-	-	-	4		
84	-	-	-	-	-	-	-	-	-	-	-	-	-		
88	-	-	-	-	-	-	-	-	-	-	-	-	-		
92	-	-	-	-	-	-	-	1	-	-	-	-	2		
96	-	-	-	-	-	-	1	2	-	-	-	-	2		
100	-	-	-	-	-	-	-	2	-	-	-	-	2		
104	-	-	-	-	-	1	-	1	-	-	-	-	1		
108	-	-	-	-	-	2	1	-	-	-	-	-	1		
112	-	2	-	-	-	5	-	2	-	-	-	-	2		
116	-	-	-	-	-	3	-	2	-	-	-	-	1		
120	-	3	-	-	-	10	-	-	-	-	-	-	1		
124	-	5	-	-	-	15	-	-	-	-	-	-	-		
128	-	2	-	-	-	4	-	-	-	-	-	-	-		
132	-	3	-	-	-	17	-	-	-	-	-	-	-		
136	-	1	4	-	-	8	-	-	-	-	-	-	-		
140	-	3	-	-	-	10	-	-	-	-	-	-	-		
144	-	1	1	-	-	6	-	-	-	-	-	-	-		
148	-	2	-	-	-	7	-	-	-	-	-	-	1		
152	-	-	-	-	-	3	-	-	-	-	-	-	-		
156	-	-	-	-	-	1	-	-	-	-	-	-	-		
160	-	-	-	-	-	-	-	-	-	-	-	-	-		
164	-	-	-	-	-	1	-	-	-	-	-	-	-		
168	-	-	-	-	-	2	-	-	-	-	-	-	-		
172	-	-	-	-	-	-	-	-	-	-	-	-	-		
TOTALS	-	22	1	-	-	95	38	10	-	-	-	-	50		

TABLE VII (Cont'd.).--Frequency Record of Juvenile Pilchards Sampled Outside California,
by Ports and by Ages.

<u>MAY, 1939</u>							
<u>Oregon</u>							
Fish length	Fish aged						Total fish measured
	From scales			From otoliths			
	Year classes						
	38	37	36	38	37	36	
104	-	-	-	-	-	-	1
108	-	-	-	-	-	-	1
112	-	-	-	-	-	-	1
116	-	-	-	-	-	-	-
120	-	-	-	-	-	-	2
124	-	-	-	-	-	-	3
128	-	-	-	-	-	-	-
132	-	-	-	-	-	-	12
136	1	-	-	-	-	-	15
140	-	-	-	-	-	-	24
144	-	-	-	-	-	-	45
148	-	-	-	-	-	-	43
152	-	-	-	-	-	-	56
156	-	-	-	-	-	-	57
160	-	-	-	-	-	-	54
164	-	1	-	-	-	-	30
168	-	-	-	-	-	-	19
172	-	3	-	-	-	-	7
176	-	6	-	-	-	-	3
180	-	3	1	-	-	-	2
184	-	7	-	-	-	-	-
188	-	2	-	-	-	-	-
192	-	4	-	-	-	-	-
196	-	3	-	-	-	-	-
200	-	4	-	-	-	-	-
204	-	4	-	-	-	-	-
208	-	3	-	-	-	-	-
212	-	-	-	-	-	-	-
TOTALS	1	40	1	-	-	-	375

Table VIII. Statistics of length frequency curves for California pilchards found from scale studies to belong to year classes 1936 to 1938.

Date	Number of specimens	Mean body length	Standard error; mean	Standard deviation	Standard error; standard deviation
<u>Year Class 1938</u>					
1938 July	44	79.27	1.59	10.52	1.12
August	74	78.69	1.30	11.22	0.92
September	65	91.07	1.11	8.97	0.79
October	69	94.66	1.81	15.06	1.28
November	42	108.59	2.51	16.26	1.77
December	50	98.94	0.90	6.35	0.63
1939 January	59	108.96	2.11	16.21	1.49
February	76	109.05	1.86	16.24	1.32
March	152	118.10	1.01	12.40	0.71
April	201	122.25	0.73	10.35	0.52
May	77	123.24	1.05	9.17	0.74
<u>Year Class 1937</u>					
1938 April	72	126.39	1.56	13.23	1.10
May	71	143.44	1.59	13.37	1.12
June	108	146.48	1.13	11.78	0.80
July	70	153.01	1.18	9.87	0.83
August	129	146.15	0.79	9.03	0.56
September	58	148.33	0.76	5.78	0.54
October	98	153.23	0.86	8.53	0.61
November	63	161.66	1.45	11.53	1.03
December	62	167.08	1.26	9.89	0.89
1939 January	99	157.62	0.89	8.90	0.63
February	132	162.59	1.01	11.60	0.71
March	180	176.01	0.62	8.35	0.44
April	108	169.37	0.94	9.78	0.66
May	95	177.60	1.10	10.74	0.78
July	183	194.17	0.93	8.44	0.66
August	150	202.55	0.60	7.35	0.42
September	90	199.83	0.95	9.06	0.68
October	43	204.15	0.67	4.41	0.48
<u>Year Class 1936</u>					
1938 April	15	149.63	2.21	8.56	1.56
May	40	165.20	1.90	12.00	1.34
June	65	168.02	1.05	8.46	0.74
July	14	172.64	3.50	13.09	2.47
August	14	165.93	4.57	17.09	3.23
September	7	158.93	3.51	9.30	2.49
October	11	163.32	1.98	6.95	1.48
November	35	186.93	2.27	13.43	1.60
December	28	178.78	1.69	8.92	1.19
1939 January	13	180.88	4.43	15.99	3.14
February	33	177.72	2.21	12.70	1.56
March	86	186.45	1.00	9.26	0.71
April	9	177.52	2.82	8.47	2.00
May	30	190.50	2.64	14.48	1.87
July	91	205.41	0.73	6.93	0.52
August	220	209.35	0.42	6.25	0.30
September	102	206.28	0.53	5.33	0.37
October	33	207.68	0.95	5.45	0.67

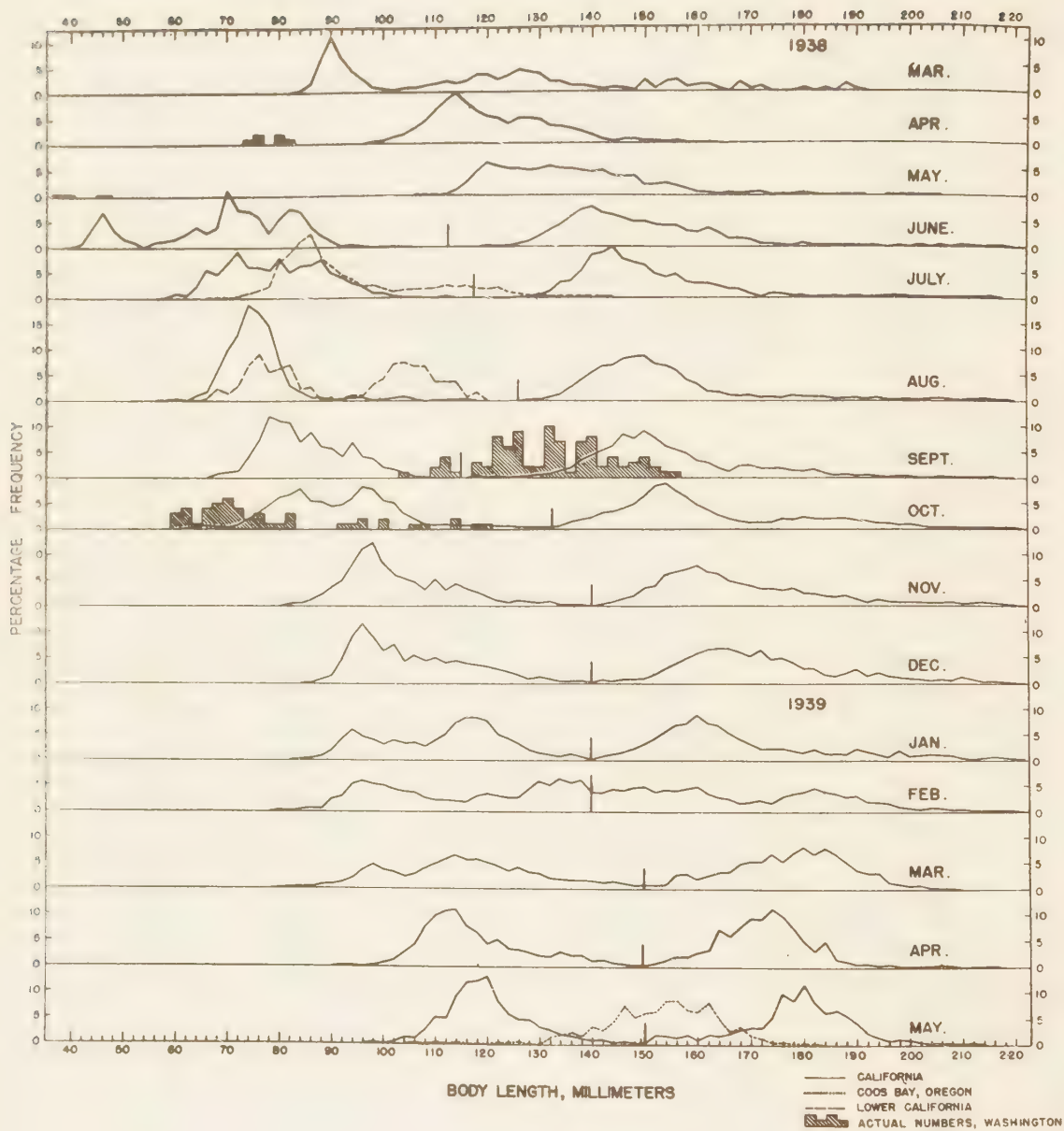


Figure 1. Frequency curves showing body lengths of pilchards sampled from the Pacific coast bait fisheries during 1938 and 1939. The samples are summarized by months.

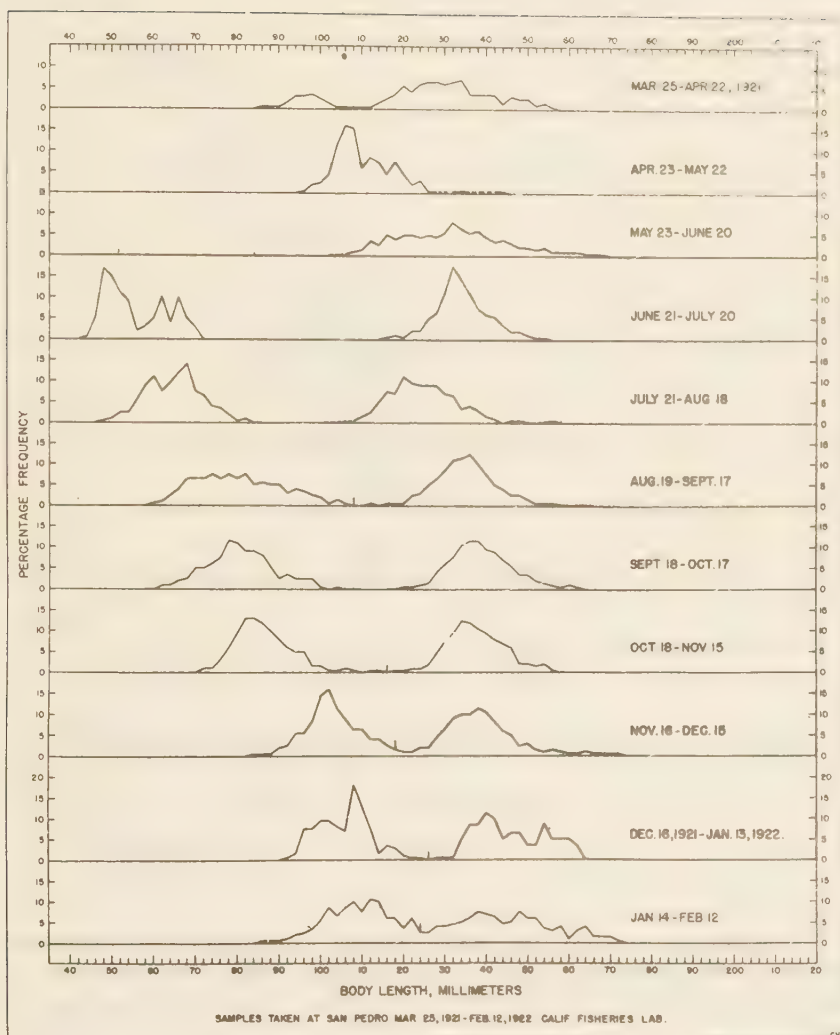


Figure 2. Frequency curves showing body lengths of pilchards sampled from bait fisheries of San Pedro from March, 1921, to February, 1922. The samples are summarized by lunar months. Original data furnished by California State Fisheries Laboratory, and discussed by Higgins (unpublished manuscript).

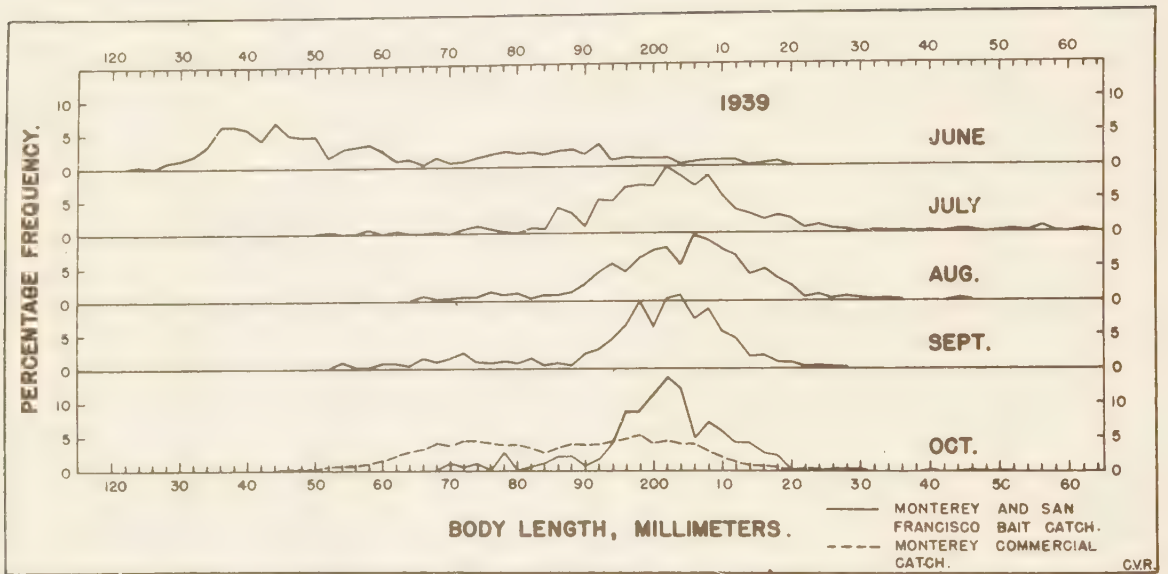


Figure 3. Frequency curves showing body lengths of pilchards sampled from central California bait fisheries, and, in October, from the Monterey commercial fishery for adults. The samples are summarized by months.

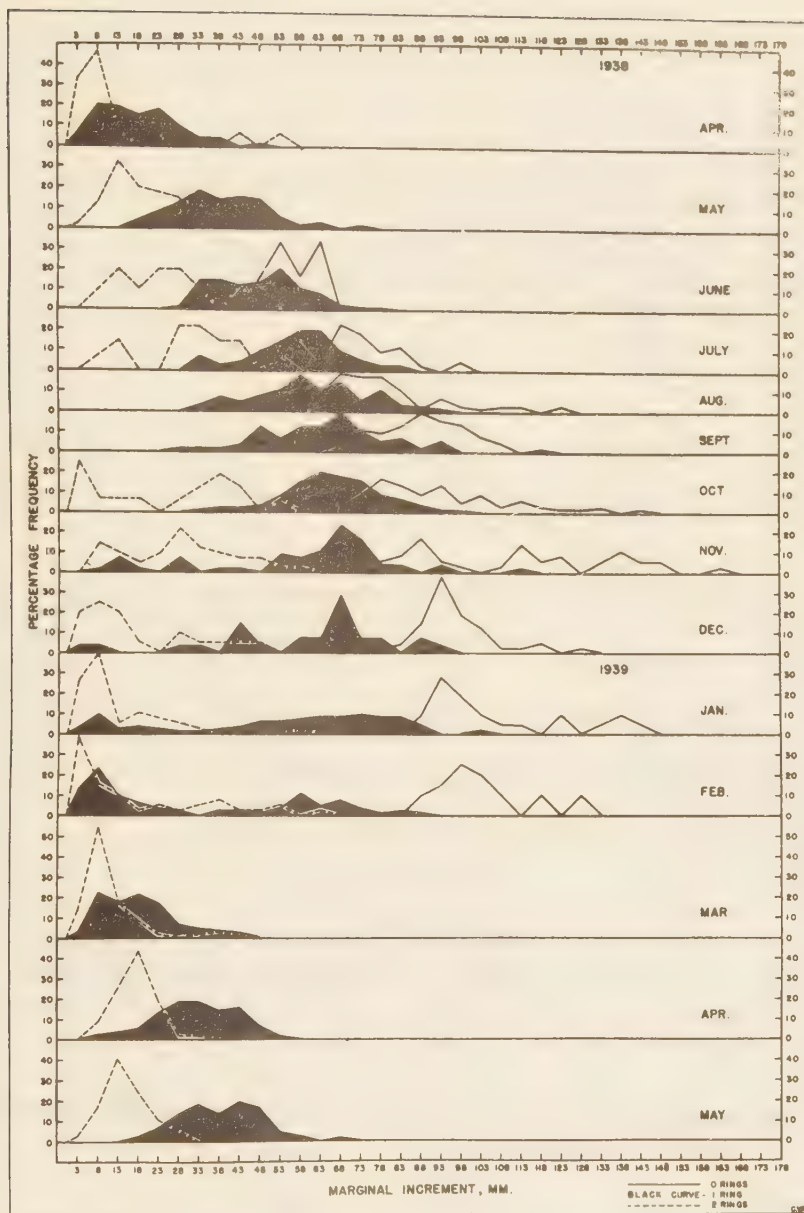


Figure 4. Frequencies of marginal increment widths in scales having 0, 1, and 2 rings. Dimensions are in millimeters of projected image; magnification is $43\frac{1}{2}$ diameters. The 32.5 mm. point is arbitrarily chosen as separating the narrow from the wide increments.

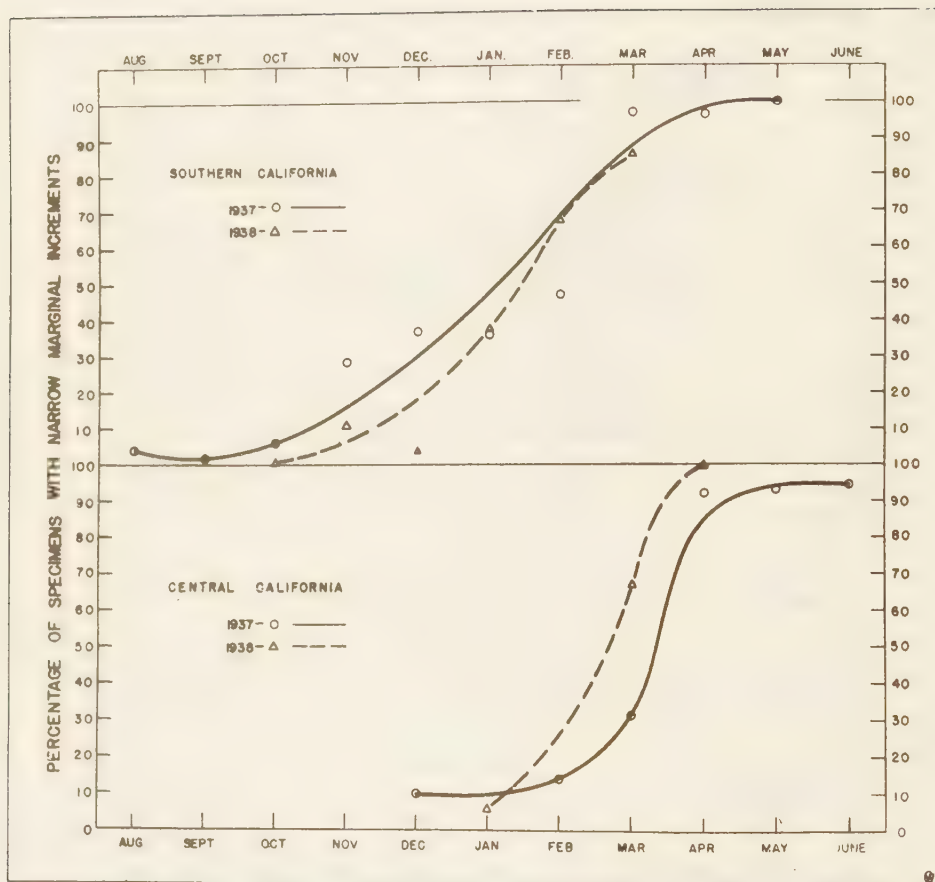


Figure 5. Percentage of scales having narrow marginal increments.

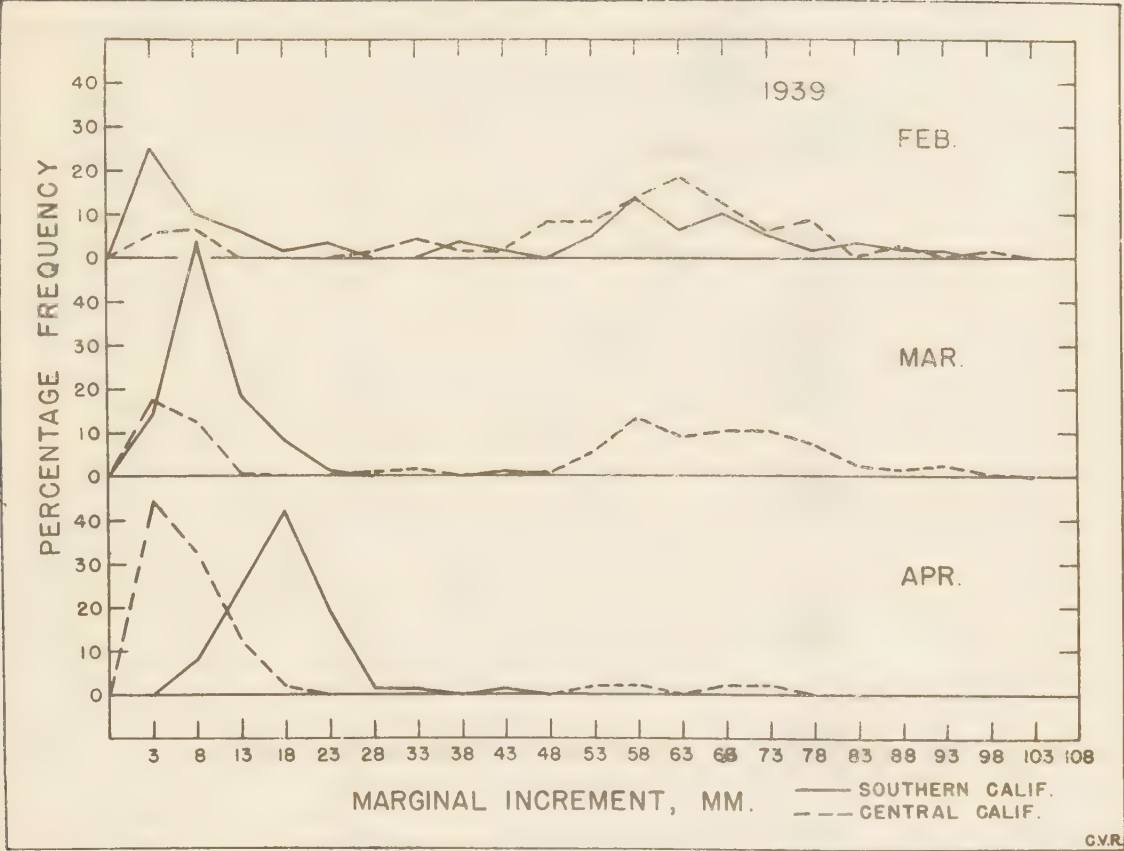


Figure 6. Comparing the widths of marginal increments in scales of fish from southern California with those from central California. Dimensions as in figure 5.

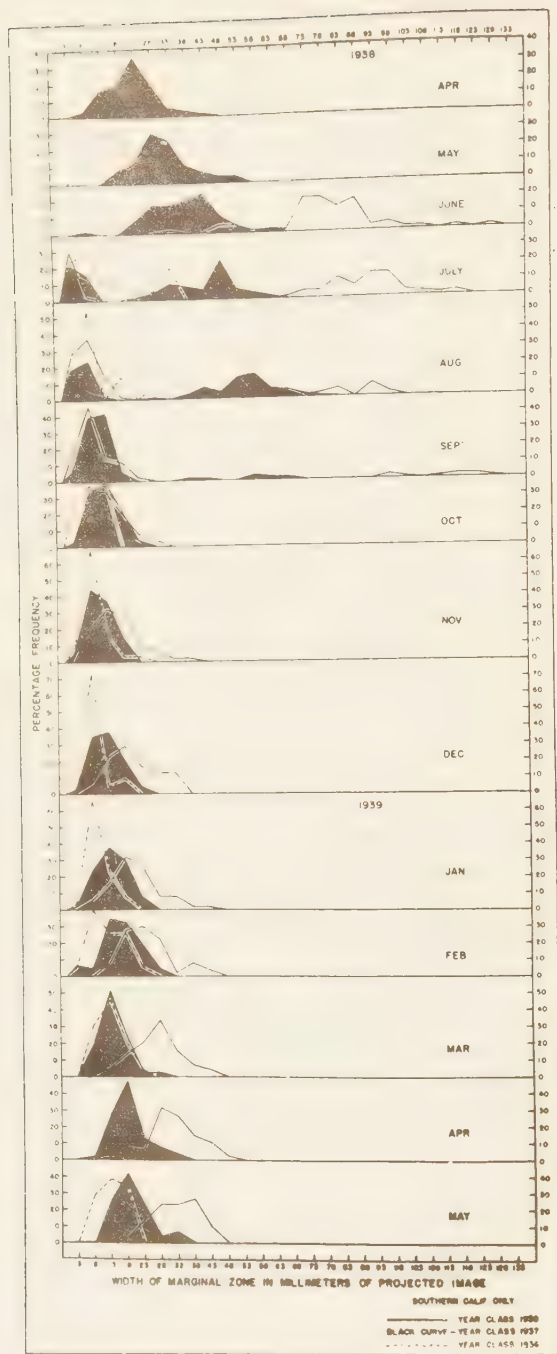


Figure 7. Frequencies of marginal increment widths in otoliths assigned to year classes 1936, 1937, 1938. Dimensions are in millimeters of projected image; the magnification is 125 diameters. The boundary between narrow and wide increments is taken as 35 mm. of projected image for specimens of year class 1938; 20 mm. for those of 1937; and 15 mm. for those of 1936.

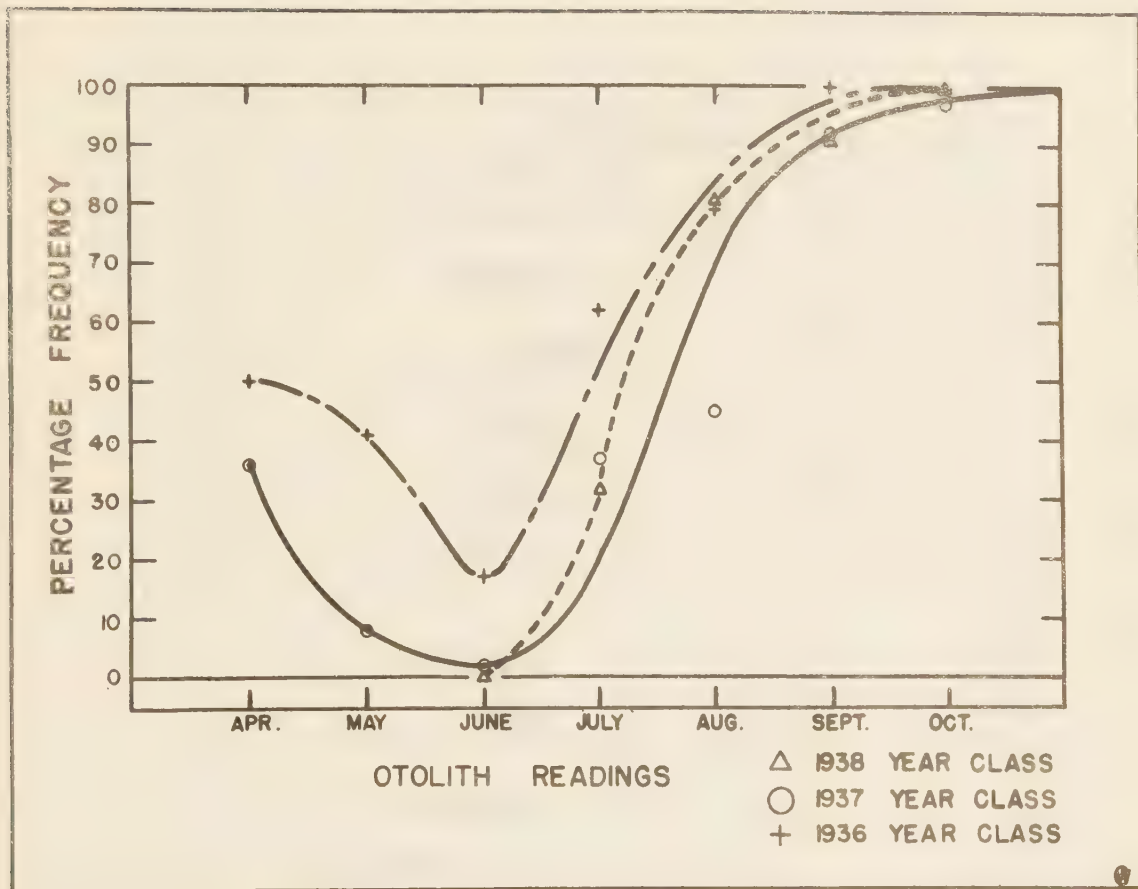


Figure 8. Percentage of otoliths with narrow marginal increments.

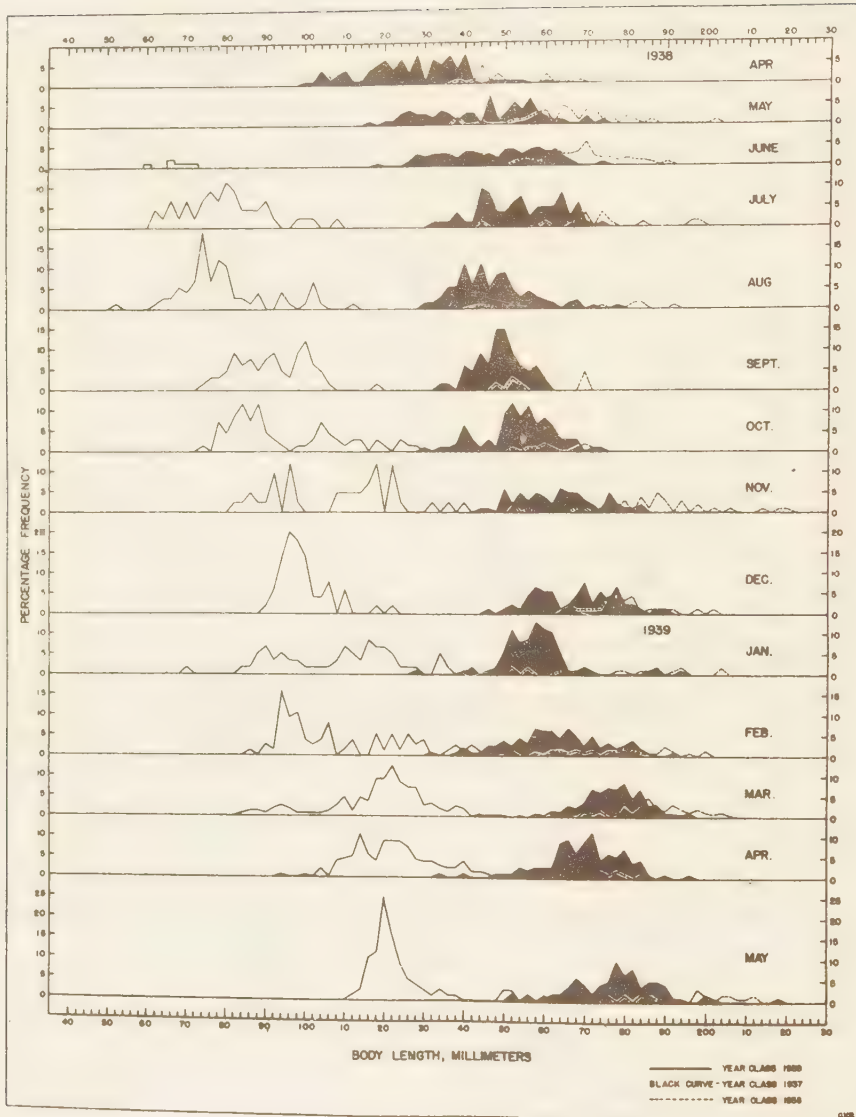


Figure 9. Showing the age composition (first three year classes only are given) of 2,600 specimens taken from California samples represented in figure 1. The ages were determined from scales.

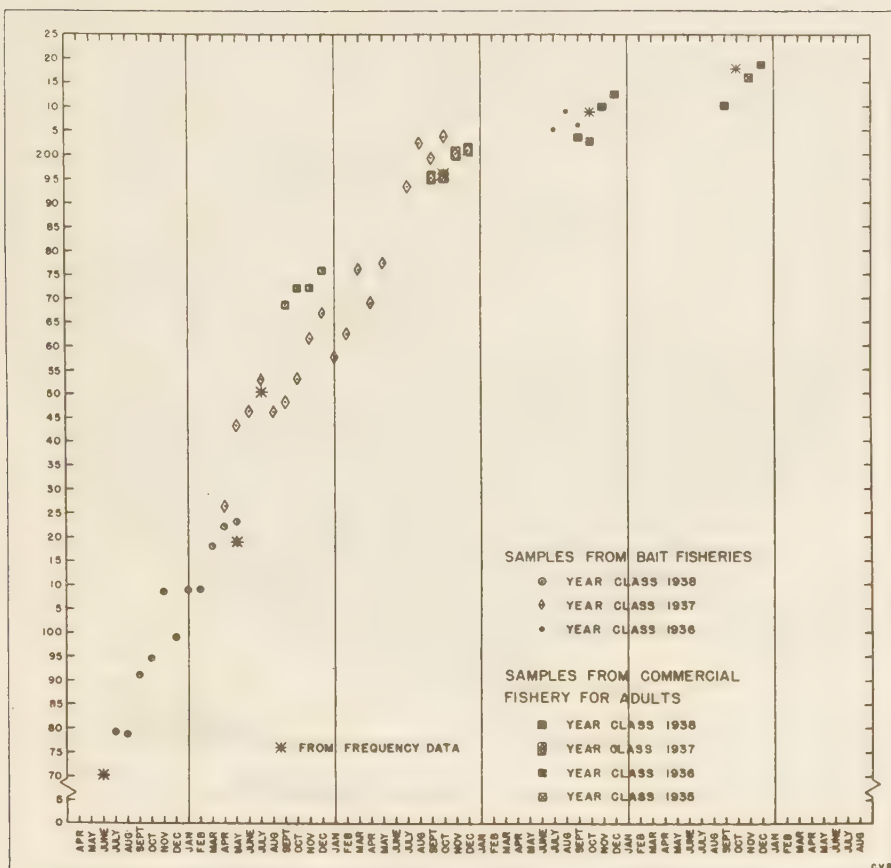


Figure 10. Mean body lengths of year classes 1935 to 1938 plotted according to age, and to time of capture. Ages were determined by scales; samples were from the California bait fisheries, or from commercial fishery for adults.

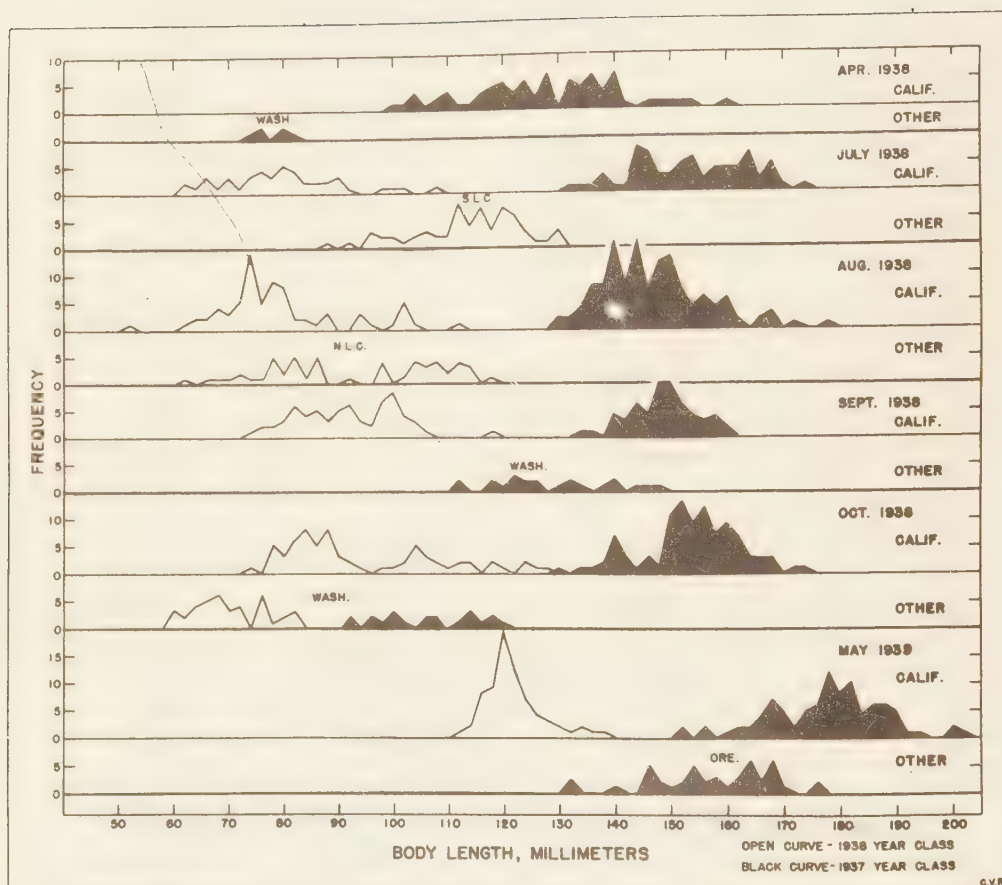


Figure 11. Comparing the body lengths of fish collected in California with those taken during the same months in Washington (Wash.), Oregon (Ore.), northern Lower California (N.L.C.) or southern Lower California (S.L.C.).

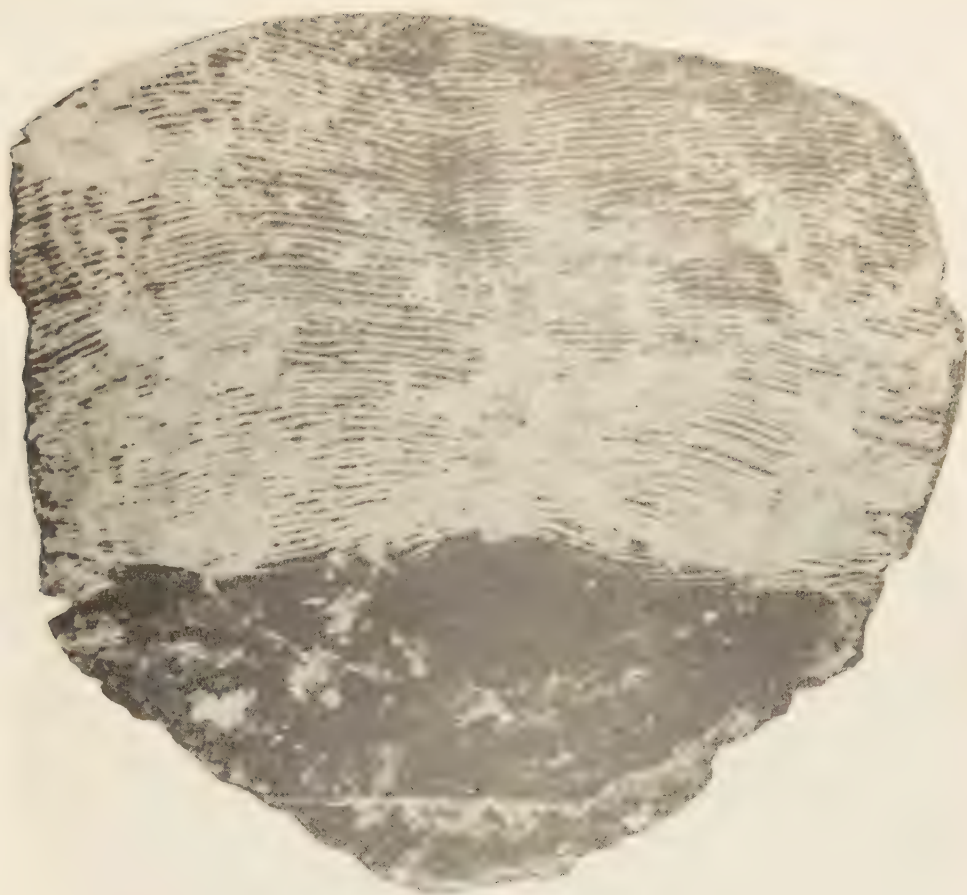


Figure 12. Above, pilchard scale with no annuli; body length of fish 63 mm.; caught June 22, 1938. Below, photomicrograph of a portion of a longitudinal section through a pilchard scale to show the surface folds.



Figure 13. A pilchard scale with no annuli. Body length of fish
144 mm.; caught July 9, 1938.



Figure 14. A pilchard scale with one annulus. Body length of fish
137 mm.; caught May 26, 1938.



Figure 15. A pilchard scale with one annulus, taken from under the lower margin of the pectoral fin. Body length of fish 123 mm.; caught April 17, 1939.

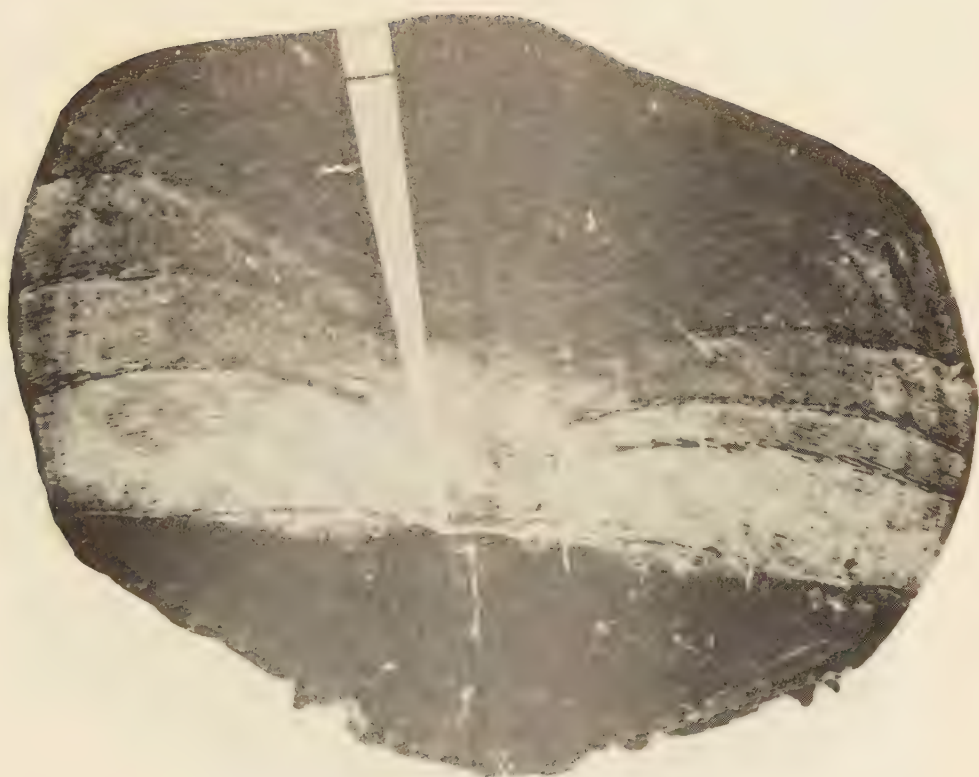


Figure 16. A pilchard scale with one annulus, which is rather obscure.
Body length of fish 134 mm.; caught January 26, 1939.

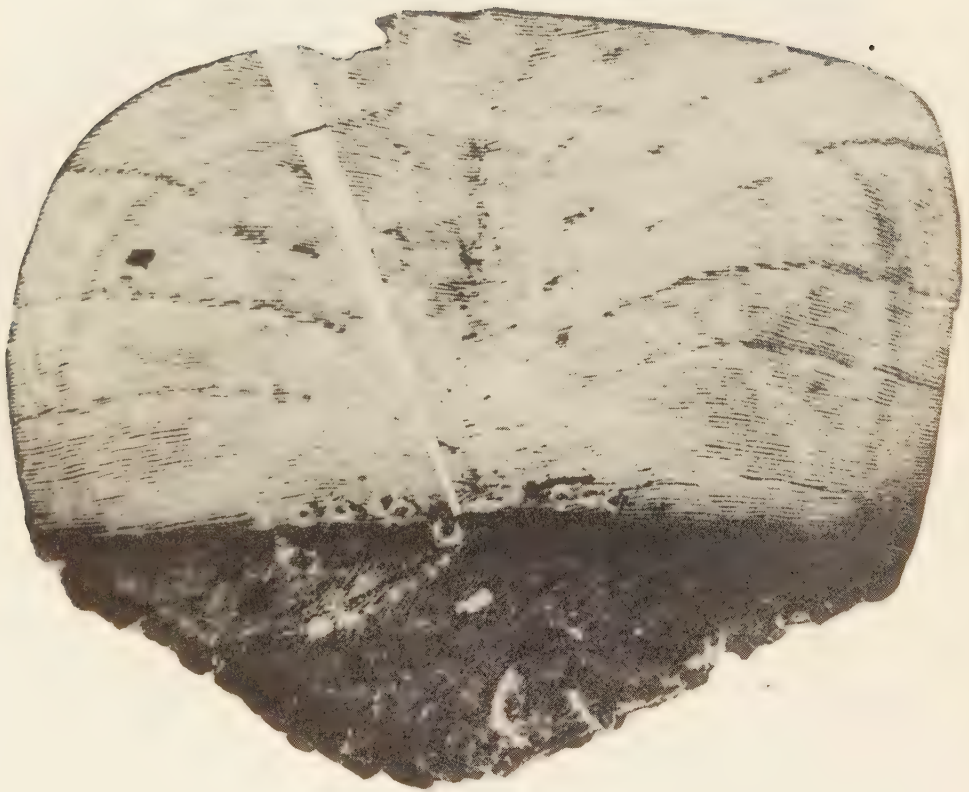


Figure 17. Pilchard scale with one annulus.



Figure 18. Pilchard scale with two annuli. Body length of fish 180 mm.; caught May 9, 1939.



Figure 19. Pilchard scale with three annuli. Body length of fish 199 mm.



Figure 20. Another scale from the same fish as indicated in figure 19, taken from under the lower margin of the pectoral fin.



Figure 21. Another scale from the same fish as indicated in figure 19, taken from the caudal peduncle.

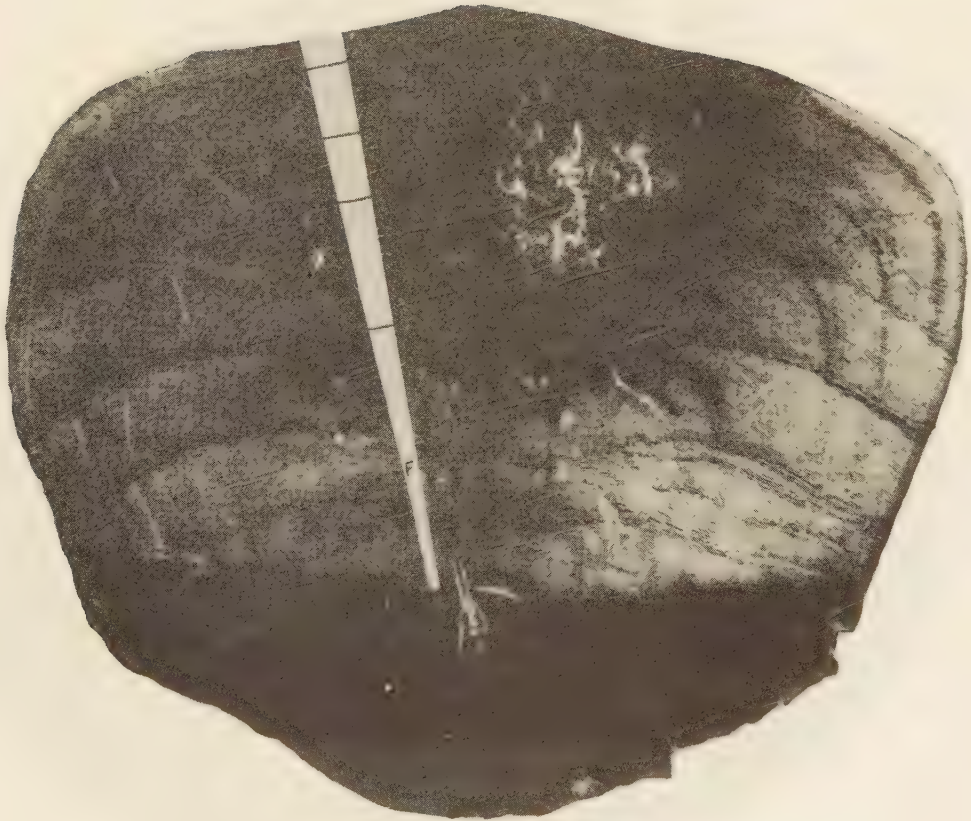


Figure 22. Pilchard scale with four annuli, and with one scar near the center (F). Body length of fish 207 mm.; caught August 3, 1939.



Figure 23. Example of a poorly marked pilchard scale, having three annuli, a false ring (F), and a scar (S) near the center, which might be confused with an annulus (but see figure 24). Body length of fish 215 mm.; caught September 21, 1939.



Figure 24. Another scale from the same fish as indicated in figure 23. Note the false ring (F), and scar-like appearance of the center, where a mark somewhat resembling an annulus appears.

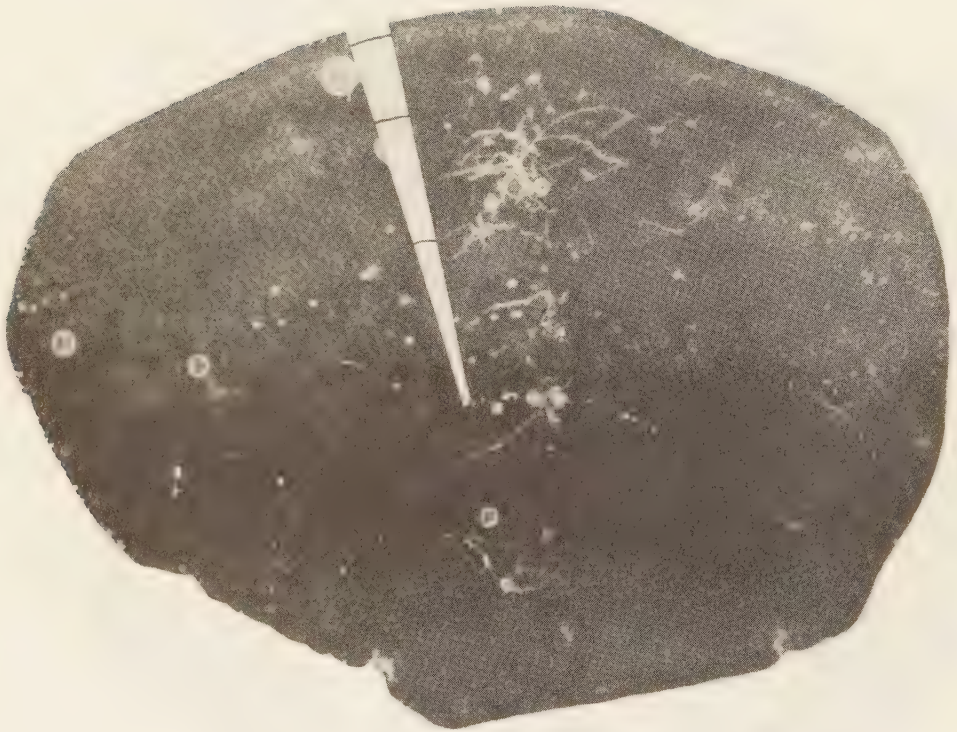


Figure 25. Pilchard scale having three annuli, mounted in glycerine. When mounted in any liquid medium, particularly those with high refractive index, pilchard scales become transparent and the surface structure loses clarity of detail. This effect increases with time, and after a few weeks, a scale so mounted becomes so transparent as to be almost completely invisible, and can then be detected only by close scrutiny at a sharp angle. Body length of fish, 215 mm.; caught August 3, 1939.



Figure 26. The same scale as shown in figure 25, here mounted dry.

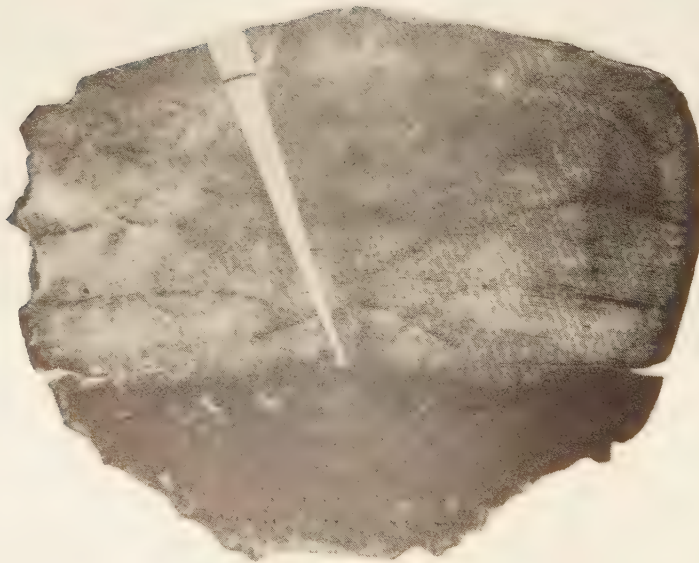


Figure 27. Two scales from a fish 111 mm. in body length, caught March 15, 1939. In the top specimen are seen clearly one annulus and two false rings, (F and S) one of which is easily confused with an annulus. In the lower specimen, only traces of the latter two marks persist, while the true annulus remains evident.

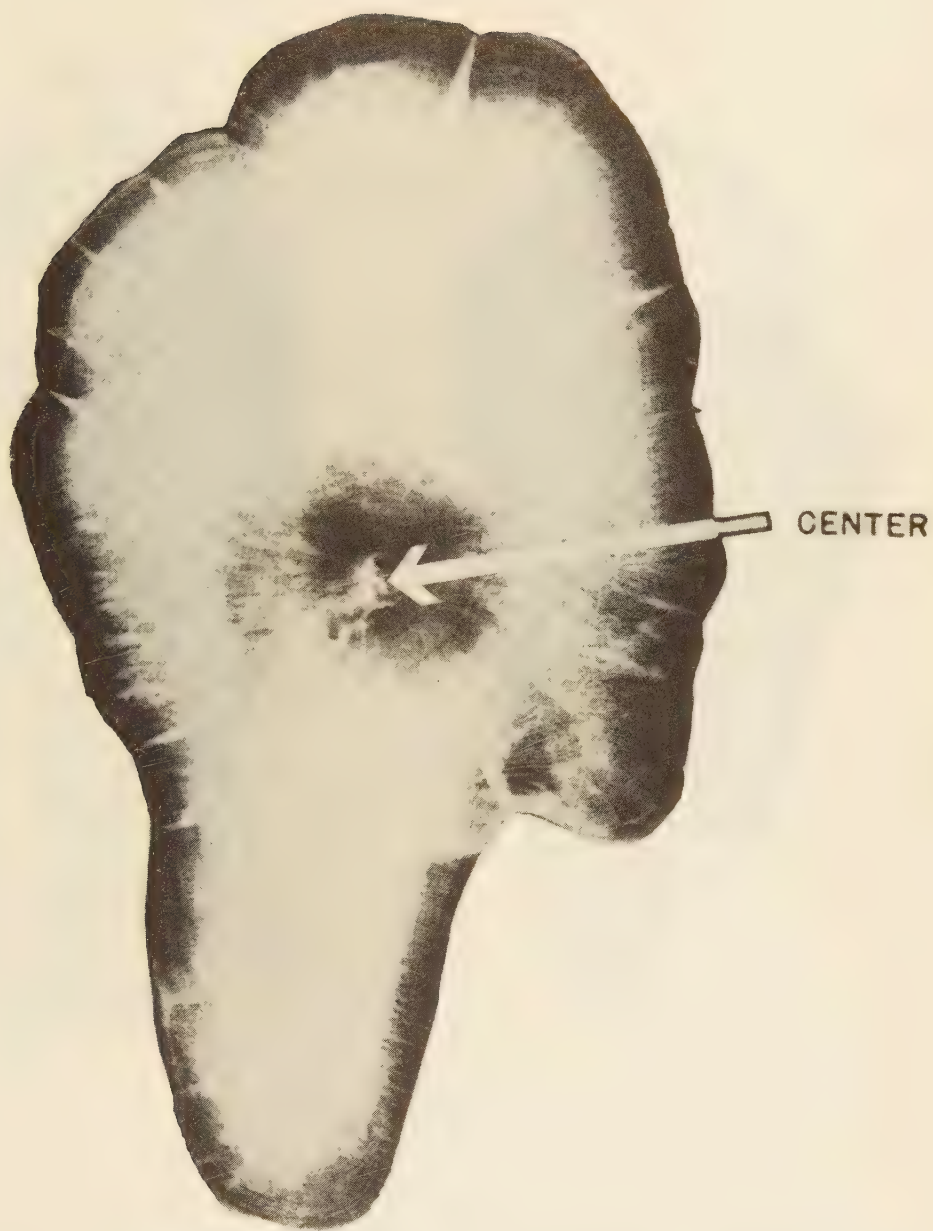


Figure 28. A pilchard otolith with no annulus. Body length of fish 70 mm.; caught June 20, 1939.



Figure 29. Left, a pilchard otolith with no annulus and a false mark (F) in the growth zone of the first year. Body length of fish 76 mm.; caught June 30, 1938. Right, a pilchard otolith with one annulus some distance from the margin, and with a false mark (F) in the growth zone of the first year. Body length of fish 121 mm. Caught May 24, 1938.



Figure 30. Left, a pilchard otolith with two annuli and a false mark (F) in the growth zone of the first year. Body length of fish 165 mm.; caught January 18, 1939. Right, a pilchard otolith with two well-defined annuli. Body length of fish 151 mm.; caught February 7, 1939.



Figure 31. Pilchard otolith with three annuli. Body length of fish 178 mm.; caught January 18, 1939.



Figure 32. Pilchard otolith with four annuli. Body length of fish 213 mm.; caught August 10, 1939.

3. Determination of Age of Adults by Scales, and Effect of Environment on First Year's Growth as it Bears on Age Determination.

By

Lionel A. Walford and Kenneth H. Mosher

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INTRODUCTION

The objective of conservation research on the Pacific pilchard, or sardine, has been stated by Sette (1943) thus: "To determine for different levels of fishing intensity (i.e., effort), the quantity and quality (sizes of fish) in the average annual catch." The statistical computations involved in this determination require a current measurement of the age composition of samples of the commercial catch. Owing to the close overlapping in lengths of fish comprising the several ages, it is not feasible to deduce age composition or even to discover with certainty the growth rate by a study of length frequency curves. To attain these ends, it is necessary to employ some other method of determining the age of individual fishes.

The scales and otoliths of the pilchard, as in many fishes, are marked with rings which appear to be related in number to age. As usual among fishes, these marks are not diagrammatically clear in the pilchard, being of various degrees of obscurity, and recognition of those that are formed only once annually (the age marks) can be easily confused by the presence of those that are formed fortuitously, the adventitious marks. In a previous report¹, the authors established criteria for distinguishing between the two types. These were critically tested on juvenile material sampled from the bait fisheries of California, and found to serve satisfactorily for determining ages up to the third year.

It is now proposed to test the application of these criteria to the scales of adult fish as taken in samples of the commercial catch, and to answer this question: With what order of accuracy can the age of a pilchard be determined by recognizing and counting the age marks on its scales? The results of this test and the answer to this question will furnish a basis for judging whether age reading from scales may confidently be used for age composition records needed in the various studies on this species.

Thanks are due to our colleagues for their critical attention and interest given during the development of this study; in particular, to O. E. Sette, who has suggested a considerable part of the methods that are new. We are grateful also to Dr. H. U. Sverdrup and Dr. W. E. Allen of the Scripps Institution of Oceanography, the former for his critical reading of that part of the manuscript touching on oceanographic matters, the latter for making available a large volume of unpublished data on diatom abundance. We are indebted, too, to Julius Phillips, of the California State Fisheries Laboratory, for his suggestions, cooperation, and criticism. The mounting of scales and a large part of the routine clerical work were done by employees from Works Progress Administration projects: 765-08-3-22, 65-2-08-286, and 265-2-08-34.

¹/ Walford and Mosher, 1943.

THE MATERIAL: ITS COLLECTION, PREPARATION AND EXAMINATION

The material for this study was collected from the commercial fishery serving reduction plants and canneries, as detailed in Table 1.

Table 1. - Source, date, and number of specimens in scale collections used for this study

Locality	Period	No. specimens aged	Agency collecting
California:			
San Pedro**	1/10/40 - 1/16/40	686	U. S. ^{1/} and Calif. ^{2/}
San Pedro**	1/21/41 - 1/27/41	761	U. S. and Calif.
Monterey *	9/20/39 - 12/21/39	3072	U. S.
Monterey **	10/21/40 - 10/29/40	998	U. S. and Calif.
Monterey **	1/24/41 - 1/30/41	241	Calif.
San Francisco*	9/10/40 - 2/41	3546	U. S.
San Francisco**	8/40	181	U. S.
Eureka **	9/40	158	U. S.
Oregon:			
Astoria*	8/7/40 - 8/10/40	140	U. S.
Washington:			
Grays Harbor *	7/19/39 - 8/17/39	789	U. S.
Grays Harbor *	8/11/40	10	U. S.
British Columbia	7/22/40 - 9/21/40	832	B. C. ^{3/}

The entire fishing seasons were sampled systematically by the Fish and Wildlife Service at Grays Harbor, Washington, in 1939 and 1940; at Monterey, California, in 1939; and at San Francisco, California, in 1940. In 1940, the Fisheries Research Board of Canada collected scales at Barkley Sound; these the board, through the courtesy of Dr. John Hart, contributed for the present study. In addition, special samples were gathered in collaboration with the California State Fisheries Laboratory at Monterey in 1940 and at San Pedro in 1940 and 1941. Other special samples were taken, as shown in table 1, for various purposes. The specimens collected at Eureka, California, were from pilchards from the stomachs of whales landed by the Whaling Station of the San Francisco Sea Products Company, and through the courtesy of the Station, sent periodically to our laboratory. In addition, scales collected in 1941 - 42 in collaboration with the California State Fisheries Laboratory, are drawn upon in this paper for illustrative or corroborative purposes.

In the regular collections a sample consisted of 50 fish, taken at random, without regard to size, from one boat's catch. As many samples were taken daily as to occupy a man's full time in collecting, measuring, and tabulating.

* Collections made in conjunction with routine sampling.

** Collections made for special purposes.

^{1/} United States Fish and Wildlife Service.

^{2/} California State Fisheries Laboratory.

^{3/} Fisheries Research Board of Canada.

Body length of the fish was measured as described by Sette (1941). For each sample, scales were obtained from the first 10 specimens having any still attached. Generally about 10 or 12 scales were taken from the side of the body near the region touched by the tip of the pectoral fin. As necessity required, however, fewer were taken, sometimes only one, and from wherever they could be found.

As the scales were collected from each fish they were placed in a small vial of water to which had been added about two drops of 2 percent phenol for preservative. The vials were kept in covered trays, 50 to a tray, and held in numbered places by round slots bored in the bottom. The collections were sent daily to the laboratory at Stanford University, where they were mounted.

Generally the field man assigned to the sampling work was able to take five samples daily, that is scales from 50 fish^{1/}. In Washington, whenever the landings were too few to permit collection of this number of samples, scales were taken from enough specimens to bring, up to that time, the daily average to 50.

In the laboratory, the scales were cleaned and dried by rubbing between the fingers, and mounted between two dry, clean slides which were then bound together at the ends with cellulose tape. The mounted scales were examined with the aid of a projecting microscope. For each specimen a paper strip printed with a millimeter measure was laid on the image along the midlongitudinal axis of the sculptured part of the scale with the zero line at the base of the sculptured part. Locations of annuli were traced on the paper strip and later recorded as dimensions after reading the millimeter measure.

These as well as such pertinent data as sample number, length, and sex of fish, locality and date of collection, name of reader, dimensions of scale, position of marks, calculated length of fish at past ages, etc., were recorded on a punch card, providing a permanent detailed record for every scale reading.

It required two hours for one person to mount 50 scale samples; two hours for one person to read 50, and about four hours for one person to tabulate the data, calculate growth increments, punch the cards, and check these steps for 50 readings. Thus the routine processes in the laboratory required about eight man hours for one day's field collection from one port.

The readings were all done by the authors. With certain exceptions, to be discussed below, each examined alternate samples of scales, Walford the odd-numbered ones, Mosher the even. By this method a check could be furnished on each man's reading, since the two sets, on theoretical grounds, should be statistically homogeneous if the operators used identical standards for interpreting annuli. The results of this check will be discussed below.

Occasionally the scale collection from a specimen was obviously contaminated with one or more scales from other fish. When that occurred, the material was discarded unless at least three quarters of the scales were obviously from the same fish, in which case these were read.

^{1/} Beginning with the 1941-42 season, an effort was made to sample approximately one-fifth of the landings.

The criteria of an age mark as set forth previously (Walford and Mosher, 1943) remains unchanged, namely:

"An annulus is concentric with the margin of the scale. It is not always a sharp or unbroken line; nor are the segments of an interrupted annulus always perfectly co-circular (if the shape of a scale may be called circular in this discussion). But the course of an annulus, continuous or broken as it may be, can usually be traced, by careful scrutiny if necessary, entirely around the sculptured part of the scale from left-hand to right-hand margins. Sometimes they can be followed even around the unsculptured part. Annuli are clearly separated from each other and do not ordinarily meet at any point. If an annulus has formed, it is present in all the normal scales of an individual."

In the scales of fish older than six years, the peripheral annuli are crowded and frequently irregular, so that they cannot be made out equally well entirely around their course, particularly in very old specimens. On such scales, the annuli are generally most distinct at the anterior "corners" of the sculptured part of the scale (see figure 1). There they are most easily located and counted, and thence they can be traced, even though with difficulty, entirely around the sculptured part of the scale. The criteria of a false year ring, given previously (Walford and Mosher, 1943) apply for older fish as well as for younger ones. These are:

"They are merely short or unassociated arcs; or if they completely circle the sculptured part, they are usually not concentric with the margin; furthermore, they frequently join an annulus at the base. In any case, they may be less distinct than an annulus, being vague and indefinite, or they may be much more distinct, having a scar-like appearance; that is, with very pronounced irregularities of pattern, the folds being broken or otherwise obviously abnormal. They rarely appear in all the scales of an individual."

ERROR OF INTERPRETING THE ANNULUS

Having established certain definitions of an annulus and of an adventitious mark, it is pertinent to learn how accurately they can be employed. Expected errors are of two types: those caused by faults of the scale and those caused by faults of the reader.

Of the first type are those cases in which a scale fails to record a year mark; also those in which an adventitious mark may look enough like an annulus easily to be mistaken for one. These cases of scale faults provide exceptions to our criteria of true and false annuli, and they are as liable to the same interpretation in a second examination as are normal scales. The percentage of errors arising from these causes probably can never be directly measured.

Of the second type are those cases in which a reader simply mis-counts the rings on a clearly marked scale; or those in which he overlooks one or more unusually obscure marks; or those in which, by faulty judgment, he miscalls an adventitious mark a true annulus. These errors are, in general, the fault of the reader, and are relatively unsusceptible to duplication in a second reading, particularly by a different reader. Therefore, the results of parallel readings may be expected to provide a measure of the personal error--the reader fault--in interpreting our criteria of year marks and in counting them.

Scales of 1,187 specimens from the San Francisco fall fishery of 1940 were read by Walford and by Mosher, each working separately and independently. Subsequent comparison showed that 1,049 or 88 percent of the pairs of readings were identical. The 138 specimens for which readings were in disagreement were then subjected to a third examination, this time by the two operators working jointly, and without reference to either of the two previous readings. On this occasion, 4 specimens were discarded as unreadable^{1/}; 123 of the joint readings agreed with one or the other of the two previous readings ("single disagreements"); and 15 were different from either ("double disagreements"). In 31 instances the "single disagreements" concerned the innermost ring, in 49, the marginal ring, and in 43, one of the intermediate rings. In terms of percentage these quantities are 25, 40, and 35, respectively. Since the average number of rings present in specimens of this group is 4.2, these percentages should be close to 25, 25 and 50 respectively, if all rings were equally difficult to recognize. Obviously, the marginal ring was more obscure than the others. Indeed, during the joint readings, it was found that uncertainty about the criteria for recognizing a newly formed ring at the margin during January and February was the cause of several of the disagreements, and a special study was indicated (see page 9).

A similar test was made by three workers, Walford and Mosher; and Phillips of the California State Fisheries Laboratory. Scales from 483 specimens, read first by Phillips, were subsequently divided into two lots, of which one was read by Walford, the other by Mosher. The two sets of readings, i.e., by Phillips and by Walford-Mosher, were identical for 431 or 89 percent of the scales. The 52 specimens for which readings were in disagreement were then subjected to a third reading, this time by the three workers together. When these joint readings were compared with the original readings, it was found that three disagreed with both Phillips and with Walford-Mosher ("double disagreements"), and 49 agreed with one or the other ("single disagreements"). Disagreements concerned the first annulus in 13 of the cases the marginal annulus in 15, and an intermediate one in 21; or, expressed as percentages: 26, 31, and 43, respectively. Thus there was no marked tendency for any one annulus to cause more disagreement than any other.

A third test with parallel independent readings was made by Walford and Mosher on 973 specimens taken from Washington. This sample contained a higher percentage of fish over three years old than those described above. For that reason, and also because the scales had not been well cleaned when collected, this test was more severe than the others. Nevertheless the two readers agreed in 709 or 73 percent of the cases. Of the remainder, 235 were "single disagreements", and 29 were "double disagreements."

^{1/} Less than 0.2 of 1 percent of the scales had been discarded as unreadable on first reading. These were specimens with regenerated centers.

Thus in three tests involving parallel readings of 2,643 specimens, there was disagreement on 454 of the cases--"disagreements"--and agreement in 2,453--"agreements." When the former were re-examined by the two participating workers, the final decision agreed with one or the other of the two original readings in 408 cases and disagreed with both in only 46.

In close to 90 percent of the cases, disagreement involved a choice of two adjacent ages, and, therefore, uncertainty as to the existence of only one of the rings; and only 10 percent involved uncertainty as to more than one ring. Save for the first of the three tests, no one annulus was the subject of disagreement more frequently than any of the others. For the first test, disagreement over the marginal annulus, which was somewhat in excess of expectation, was later corrected as a result of a special study (see page 9).

A reader's decision as to which of two adjacent ages a "disagreement" should be referred, might possibly be determined by chance. Assuming this to be true, half the specimens should be assigned to the younger age, half to the older. Consequently the size composition of fish comprising the two halves should be statistically identical, and should agree equally well or badly with the size composition of the "agreements" of the two adjacent ages in question. To examine this hypothesis, a series of chi-square comparisons was made, the results of which are summarized in table 2. The tabulated figures give the probability of obtaining, in a second series of samples, differences in size composition as great or greater, by random error.

Table 2.-- P values obtained on chi-square comparison between size composition of agreements and revised disagreements.

	Final determination on revised disagreements							
Agreements, number of rings	Number of rings							
	3	4	5	6	7	8	9-	
3	:.74(2) ^{1/}	:.001(2)						
4	:.004(2)	:.26(3)	:.001(5)					
5		:.001(4)	:.16(7)	:.001(5)				
6			:.0015(6)	:.08(5)	:.001(4)			
7				:.001(4)	:.90(5)	:.001(4)		
8					:.001(3)	:.72(2)	:.00(1)	
9						:.01(2)	:.60(1)	

^{1/} Figures in parenthesis indicate degrees of freedom.

According to table 2, the size distribution of the fish yielding "agreements" on a given age, when compared with that of fish assigned to that same age by revision of readings that had originally disagreed ("revised disagreements"), gave P values high enough to indicate that the two distributions had been of the same population in the statistical sense. On the other hand, when a parallel comparison was made with adjacent year classes, the P values were all so low that there could be no question that the fish were of different populations in the statistical sense. It appears, then, that the final decisions on the disagreements were not determined by chance, but must have been, on the whole, corrections of errors in the first reading.

It is, of course, not possible to know the absolute error of the final determinations. Among the "agreements" can be erroneous readings that agree by chance; but for scales of ordinary difficulty the number of these is probably low, being something less than one percent of the cases^{1/}. In addition, there must be errors among the joint readings.

There may be more of these than are found among "agreements," since only the more difficult scales tend to be the subject of disagreement. Furthermore, the final decisions in the joint readings may be determined often by the domination of one of the participants. Finally, there are the errors resulting from scale faults, referred to above.

Errors from all these causes are not measurable by any known methods. The material and methods at hand provide merely this incomplete measure: If B disagrees with A, A is not held to be in error if a joint reading concurs with him rather than with B. Hence, an index of a reader's error is the number of age determinations with which there is disagreement in both a parallel reading and in a subsequent joint reading, expressed as percentage of the number of specimens aged. For the three tests discussed above, this index of error, by ages and by three readers, A, B, and C, totalled as given in table 3.

Table 3. - Index of error

Number of rings	Number of specimens read by reader		Number of errors by reader		Index of error by reader					
	A	B	C	A	B	C	A	B	C	
1	66	66	26	1	2	6	1.5	3.0	23.0	
2	272	225	318	5	5	13	1.8	2.2	4.1	
3	862	853	112	22	39	8	2.6	4.6	7.1	
4	684	683	20	49	62	4	7.2	9.1	20.0	
5	253	235	7	28	29	1	11.1	12.3	14.3	
6	164	181	0	12	33	-	7.3	18.2	-	
7	62	66	0	14	20	-	22.6	30.3	-	
8	31	40	0	4	7	-	12.9	17.5	-	
9	33	27	0	9	10	-	27.2	37.0	-	
	2,427	2,376	483	144	207	32	5.9	8.7	6.6	

^{1/} This is based on the average known error of each man being close to seven percent. The probability of both misreading any one scale on the average, assuming purely random error, is $(0.07)^2 = .0049$.

Table 3 gives evidence that the index of error varies from age to age, being higher for the older than for the younger classes; and, therefore, the error on age composition must vary according to the number of old fish present. The index of error varies from reader to reader; also for any given reader, from time to time, being more or less proportional to the degree of his fatigue. It has been our experience that readers sometimes unconsciously adopt faulty reading techniques which result in their making some types of errors consistently over a period of time. Thus, Reader C (table 3) tended during the test to overlook the marginal ring on scales with two annuli, and consequently he recorded an excess of yearlings. Faults of this kind are detected and eliminated during the joint readings.

To avoid such errors, frequent tests should be made. Indeed, it would be desirable to make parallel readings of all scales were it not impractical in routine work involving several hundred specimens weekly. Fortunately, at least 95 percent of the California catch is composed of fish younger than 5 years, for which the index of error is low enough to justify substituting for parallel readings the procedure described below. For the remainder, the relatively high error necessitates making parallel readings on all specimens.

In the light of the foregoing results, the following procedure was adopted for future routine work: The slides will be dealt among the several readers like playing cards, so that all have equal-sized, randomly distributed portions that should prove to be statistically identical as to body length composition. That being true, the age compositions of the several portions should also be statistically identical; and significant differences among them should be detectable by the chi-square test, as described below. Wherever such differences occur, the scales will be re-read and the cause of the differences found and corrected. Meanwhile, specimens aged as five years or older will be given parallel readings; and joint readings will then be made of the disagreements.

Following this procedure, the scale collections taken during the 1940-41 season at San Francisco, 3,210 in number, were dealt between Walford and Mosher. That the two portions were statistically similar in size composition is indicated by a chi-square comparison, which gave a probability of 0.58 that a second pair of samples drawn from the same population would differ in size composition as much or more by chance alone.

For the same reason, if these two random portions were alike in size composition, they should be alike in age composition. A chi-square comparison was therefore made between the totals of each year class in Walford's portion and those in Mosher's. This test gave a probability of 0.13 that a second pair of samples drawn from the same population would differ in age composition as much or more by chance (chi-square was 8.4 with 5 degrees of freedom). Though high enough to be acceptable as evidence that Walford and Mosher had, in the main, read their respective lots of scales alike, it is at the same time low enough to suggest the presence of some non-random differences between the two series of age distributions, due, possibly to some difference in the interpretations of the two readers.

To learn then whether such a difference might be centered about fish of certain size categories, a chi-square comparison of age composition was made for each size class.

For this purpose, size classes were made as small as possible--usually two millimeters--but large enough to contain, for each member, a minimum of ten specimens. The results of this analysis indicated no significant differences between the two readers--all P values were well above .05--except for eight classes in the size range 211-226 millimeters. For each of these was indicated a probability of less than 0.001 that a second pair of samples from the same population could differ as much or more by chance. Accordingly, scales of the 1,131 fish in this size range were reexamined, the two readers exchanging their respective portions so as to check each other's first interpretations. It transpired from the subsequent joint readings of the disagreements, that the chief cause of disagreement had been confusion as to the criteria for distinguishing between old and new rings at the margin, particularly during January and February, when accelerated growth is exposing the newly formed annulus.

This difficulty was at length resolved by a special study as described on pages 9 to 11, which provided an objective method of making the necessary distinction. After the method had been applied, the two original portions, Walford's and Mosher's, were again compared as to age composition, by the chi-square test. On this occasion the probability was 0.44 that the two distributions would differ as much or more by chance in a second pair of samples drawn from the same population.

Thus an equivalent of parallel reading has been devised, which saves considerable labor, yet serves to detect and correct errors in the interpretation of the criteria of age marks. The method was applied during the 1941-42 season, when three persons were employed. The average P value obtained on first readings was .48, indicating no significant difference in results among the three readers $\frac{1}{2}$.

RECOGNITION OF THE NEW ANNULUS

In a previous paper (Walford and Mosher, 1943), it was shown that the new annulus appears on the scales of young pilchards, up to three years of age, from late fall to early spring. Judging from the present data, it appears at the same season in the scales of adults. Because commercial fishing

I/ It has been suggested by those critically reading the manuscript of this paper that the above discussion tends to over-simplify age determination of pilchard scales. It must be emphasized that a considerable degree of judgment must be exercised in recognizing age marks. This requires skill obtained from experience illuminated by knowledge of the biology of growth. It also requires much patience and a certain sympathetic attitude toward scale reading. Nevertheless, the evidence described on pages 11ff was obtained despite the subjective nature of these imponderables. It appears, however, that age reading cannot be practiced equally successfully by all investigators.

for adults is carried on only from late July or August to February or March, and fish in sufficient quantity for study are not available during the intervening time, it is not feasible to follow an entire year's cycle for adults as it was for the young. In July, however, when specimens were first taken, the last ring was found to be fully formed in all examined, and was completely surrounded by a narrow marginal growth zone; and no specimens were found with developing new rings. During succeeding months the margin beyond the last ring seemed to increase in width, and by late fall new rings began to appear in a few specimens. While these were in the process of formation, they could be easily distinguished from old rings by the following criteria:

an annulus is recognized as forming when it does not appear entirely around the sculptured part at once, but generally only on the most distal parts of the edge (see figure 3); or, when it extends entirely around the sculptured part, it touches the edge at one or more points.

These criteria seemed to serve for distinguishing new rings until about early January. From then on, however, an increasing number of specimens occurred with the last (submarginal) ring remarkably close to the edge of the scale, but complete, and entirely bounded by a marginal zone. For these the above criteria could not be applied. Instead, at the time of first reading, the operators tried to judge whether they were new by whether or not they were at any point of their course obviously closer to the edge than could be accounted for by a year's growth. Unfortunately, there are intermediate cases which could be attributed equally well to a year of abnormally slow growth or to a few weeks of abnormally rapid growth. Consequently, the decisions on these cases rested more or less with chance, and as shown by the studies on parallel readings, this was one of the chief causes of disagreement among the readers.

In an effort to devise an objective standard for distinguishing new from old rings, therefore, a statistical study was made on the width of the marginal growth zone. One would expect the latter to be narrowest shortly after a new ring has formed; and to increase thereafter in width during the year, reaching its maximum just before the following new ring appears (Walford and Mosher, 1943). Accordingly, the distance between the last annulus and the edge of the scale--the marginal zone--was measured to the nearest 0.2 millimeter of projected image (equivalent to 0.00667 millimeters in actual width), on all scales taken from July 1940 through February 1941.

These data were tabulated by number of rings (not by assigned year classes), according to width of margins, in the form of a frequency distribution. For example, all scales having four rings were tabulated together. It would be expected that early in the season, they would all be of year class 1936; later in the season some of them (those with new rings) would be of year class 1937. The two groups would be expected to have the same relative variation about their respective means, and to put this on an absolute basis for purposes of graphical study, sizes were converted into logarithms, which were tabulated into classes of equal intervals (Schrek and Lipson, 1941). In figure 5 the results of this transformation are given for scales with four rings, as an example of a case of average difficulty. A dominant mode to the right, which can be followed through the season, is taken to represent the margins attributable to the past season's growth; and a new mode to the left, appearing in November, probably represents margins attributable to the next season's growth.

These data have been fitted with normal probability curves, according to a graphical method devised by O. E. Sette (unpublished manuscript). A single normal curve fits the data for July-August and for September-October. This group is assigned to year class 1936. It obviously persists through the season, retaining certain consistencies, namely, first, a mode which advances slightly, indicating slow autumnal scale growth; second a standard deviation which remains constant. For November-December, and for January-February, it was necessary to add a second, overlapping, curve on the left. This group is assigned to year class 1937. As in the right-hand group, this too has the characteristics of a mode which advances, as is to be expected, from scale growth, and a constant standard deviation.

To measure the degree to which the selection and placing of these hypothetical curves fit the empirical data, comparison was made by the chi-square method. A P value of .06¹/₁ was obtained, (chi-square = 30.4; degrees of freedom, 19), of borderline significance.

Chief contribution to the chi-square comes from the sixth to ninth classes. It appears, then, that the low P value first obtained was due to minor irregularities of the data, rather than to selection and placing of the hypothetical curves. If these be combined, the seventh class with the sixth, the ninth with the eighth, P becomes .56 chi-square 15.59; degrees of freedom 17).

This, then, is an objective means of allocating proportions of new to old rings where the marginal increments overlap. In the four-ring series (Fig. 1) allocations were made as follows for November-December: To the older age, 1/6 the specimens in size-class 7, 3/4 in size-class 8, 34/35 in size class 9. The remainder in these classes were assigned to the younger age. In January-February, to the older age were allocated 9/26 of the specimens in size-class 8, 31/38 in size-class 9. The remainder in these classes were assigned to the younger age.

The assignment of ages to individuals in these critical cases by the method just described, precludes using those individuals for other studies involving sizes, ages or growth, and the statistical cards were marked accordingly.

This method of solving the problem of distinguishing between new and old rings has been incorporated into the routine of age analysis in pilchard research.

EVIDENCE BEARING ON THE VALIDITY OF SCALES FOR DETERMINING THE AGE OF ADULT PILCHARDS

The foregoing section has dealt exclusively with the question of how correctly one or more scale readers can assign a given age to a given fish, or to the measurement of the "reader error". In the following discussion the effect of this error plus that of the scale error (cf. page 4) will be examined.

¹/₁ I.e., the probability is .06 that a second series of empirical data would differ as much or more from this theoretical series of curves, by chance.

The annual occurrence of age marks in pilchards of juvenile age had been proved in the following way¹: A stratified random sample of scales was prepared to represent equally all the months of the year. The labels on the slides were then masked, the slides mixed, and the scales examined and measured without knowledge of the size of the fish or the time of year collected. When the measurements thus obtained were collated, it was found that the marginal increment was narrower at one season--the spring--than at any other, and increased in width during the remainder of the year. Its growth was rapid in spring and early summer following the formation of the annulus in the winter, and slight from late summer to winter.

The foregoing demonstration was possible because young pilchards are available near shore in California throughout the year and are taken by the bait fisheries. "Adult" pilchards, on the other hand, are migratory, departing for their spawning place at the time of maturity, in the spring, and not reappearing until mid-summer. Hence, the commercial fishery for adults is seasonal, and the scale material collected for this study does not include an important period of the year's growth. Despite this hiatus in data, the results discussed on pages 9ff and given graphically in figure 5, indicate, as far as they go, that in adults, as in the young, the annulus appears during one season of the year--the winter, and that the marginal increment increases in width until the next annulus is formed.

For critical proof of the validity of scale reading, the annual growth increments on the scales were studied in search of peculiarities in dimensions, marks or other irregularities associated consistently with certain year classes such as Lea had discovered for the Norwegian herring (Lea 1919). To provide homogeneous data, an effort was made to select scales consistently from the same part of the body, namely the side, near the tip of the pectoral fin. Unfortunately such selection was unfeasible whenever the fish sampled were in poor condition. Under these circumstances, scales were taken wherever they could be found, often from the back or near the caudal peduncle, where pilchard scales are characteristically smaller than elsewhere. For adjustment to a common basis to permit comparative studies, therefore, scale measurements were translated into terms of body length of the fish, by means of Lea's formulae:

$$\frac{s_n}{S} = \frac{f_n}{F}, \text{ and} \quad (1)$$

$$f_n - f_{n-1} = t_n \quad (2)$$

Where s_n is the distance from the center of the scale to a particular annulus, n ; S the distance from the center of the scale to the edge of the scale; f_n the length of the fish at the time the annulus n was formed; F the length of the fish at the time of the observation; t_n the growth increment in the year preceding the time the annulus n was formed. Hence, $t_1 = f_1$; $t_2 = f_2 - f_1$; etc. The symbol "f" is the same as Lea's "l"; it abbreviates the term "fish length" as "s" does "scale length".

¹/ Walford and Mosher, 1943.

This formulation assumes simple, perfect correlation between body length and scale length, with a regression having its origin at zero. It was found, however, that the assumption is no more valid for pilchards than for many other fishes studied. The scales are not formed until the fish has reached a length of 3 to 4 centimeters. For a time thereafter, until the body becomes fully scaled, the growth rate of the scales is rapid in relation to that of the body; then it decelerates, until at length the slope of the regression, b, becomes constant. This occurs below the minimum length of fish found in our samples. Hence, for the material used in this study, the relation of scale length to body length may be expressed by a simple straight line regression of the type $y = a + bx$, and Lea's formula (1) must be modified to:

$$\frac{s_n}{S} = \frac{f_n}{F} + a \quad (3)$$

For calculating a, the regression of scale length on body length was plotted separately for each of four year classes, those of 1936 to 1939, to which specimens had been allocated by scale studies.

The values of a and b were as follows:

Year Class	<u>a</u>	<u>b</u>
1936	-2.2378	.7326
1937	0.8464	.7285
1938	-20.3317	.8405
1939	2.0814	.7240

Significance of differences, in terms of $P^{\frac{1}{2}}$ (according to Fisher's t test) is as follows:

Year Class	Compared with Year Class		
	1939	1938	1937
1936			
<u>a</u>	.30-.40	.01	.40-.50
<u>b</u>	.50	.01	.50
1937			
<u>a</u>	.50	.01	
<u>b</u>	.50	.01	
1938			
<u>a</u>	.01		
<u>b</u>	.05-.10		

In regression of scale length on body length, year classes 1936, 1937, and 1939 did not vary from each other beyond the range of random error; but year class 1938 differed significantly from each of the other three, both as to a and b.

^{1/} That is, the probability that if an additional pair of samples be drawn from the same population, they would differ as much by chance as the two under comparison, or more.

Thus the fish assigned to one year class had an intrinsic quality in common in addition to the number of rings on their scales, peculiar to their class, which persisted during three years of this study. It is fortunate that this peculiarity applies to year class 1938, for it is that class on which the most complete collection of material is at hand, going back to first appearance in the bait fisheries, when identification of its age as fish of the year was virtually beyond question. And it is that class from which the material was drawn on which the validity of age determination of juvenile pilchards was proved (Walford and Mosher, 1943). Thus fish identified with certainty as belonging to year class 1938 have been marked by Nature with a characteristic that may continue to serve for distinguishing them as a group for several additional years.

Since the relation of scale length to body length can vary among year classes, it is necessary, for approximating past growth as accurately as possible, to determine a for each year class separately. To do this requires measurements over a sufficient range of sizes - therefore years of growth - to provide a significant measure of the regression. With present material, this was possible only for the four year classes mentioned above. Consequently, in the following discussion, averages concerning those year classes alone have been adjusted as of formula (3) (page 13); and with the appropriate a values (page 13). For the rest, formula (1) has had to suffice.

Summarizing: To detect important anomalies in the past growth of the several year classes, the lengths at the past ages (f_n) were calculated by Lea's formula (1). These were averaged, and averages for year classes 1936 to 1939 were adjusted to take into account departures from exact proportionality of scale length to body length; in other words for the failure of the regression of scale length on body length to intersect with coordinates $0, 0.1$. Values of $\bar{f}_n$ were obtained by subtracting $\bar{f}_n$ from $\bar{f}_n - 1$.

The results of these calculations for the first year's growth increment ($\bar{f}_1$), given in Table 4, are remarkably variable. Among year classes 1932 to 1938 collected in 1939-40, for example, the average first year's growth increment ($\bar{f}_1$) ranged from 98 to 115 mm. Such apparent inconsistency could be caused by changes with age and size in the scale length-body length relationship. It could also occur if increasingly larger portions of the size range of each year class became available to the fishery as the year class became older. Or it might result from systematic errors in marking the location of the annuli, which were somehow associated with age.

1/ These adjustments were made graphically as follows: The average total length of a year class under consideration was located on the scale length-body length regression line, and a line drawn from there to the origin of the graph. Each $\bar{f}$ value for that year class was then located on the latter line; and the intersection between the ordinate passing through that point, and the scale length-body length regression line gave the adjusted value of that $\bar{f}$.

Table 4. - Average calculated first growth increments, by year classes

Year class	Average calculated length for fish collected in season of -					
	1939-40		1940-41		1941-42	
	Unadj. <u>1/</u>	Adj. <u>2/</u>	Unadj. <u>1/</u>	Adj. <u>2/</u>	Unadj. <u>1/</u>	Adj. <u>2/</u>
1932	111.83		108.97		110.00	
1933	114.02		115.20		111.26	
1934	102.22		107.04		106.48	
1935	104.49		107.62		103.84	
1936	97.95	99.4	101.98	103.0	102.74	104.3
1937	113.91	114.4	113.76	114.1	112.03	113.6
1938	115.14	123.6	108.93	118.5	99.89	113.0
1939			102.66	102.0	92.91	92.0
1940					116.73	

1/ Unadjusted figures.

2/ Adjusted for deviations from exact proportionality of scale length to body length.

It is reasonable to expect that all these causes would be progressive and rather regular in their effect, resulting in constant increase or decrease in comparable values of $\bar{t}$ with increase of age. Also, this trend should be continued in the collections of later years.

It is apparent at once from table 4, however, that far from progressing regularly, the comparable values of $\bar{t}$ fluctuated with no evident order in each of the three years of data studied. Thus it seems improbable that the fluctuations could be associated with age. On the other hand, it does appear that they are associated with year classes. If so, any given growth increment ($\bar{t}_n$) of a given year class should deviate from a norm of that increment in the same direction every year, as long as that class is wholly and significantly represented in the samples with respect to the increment in question. The meaning of this will become clear presently.

To establish a norm for $\bar{t}_1$, the $\bar{t}$ -values for year classes 1932 to 1938, inclusive, were averaged, using the material collected during the season of 1939-40, and these grand averages were taken as norms for that season. Deviations of the $\bar{t}_1$ values for individual year classes were then plotted as curve number one in figure 6. The same procedure was followed with the material collected in the next season (1940-41), furnishing a second curve in figure 6. Although an additional year class, that of 1939, was present, it did not enter into that season's norm; but the deviation of its $\bar{t}_1$ value from the norm is indicated by a dotted line. Next the material collected in 1941-42 was similarly treated and the results plotted in the third curve of figure 6. Year class 1939 was not included in the norm, but deviations of its $\bar{t}_1$ value is indicated in figure 6 by dotted lines.

These three curves are closely similar. In all three, the first year's growth increment for year classes 1933, 1937, and 1938 deviates above the norm. In six out of seven points all three curves are in agreement. The probability that such agreement could occur by chance is slight.^{1/} In the absence of random occurrence, then, the agreement must mean that specimens having certain growth characteristics in common were allocated consistently to the same year classes three years in succession. It remains to be shown whether the allocation was correct.

EFFECT OF ENVIRONMENT ON THE GROWTH OF THE PILCHARD, AND ITS BEARING ON AGE DETERMINATION

If the anomalies described in the preceding section are a characteristic of the year classes, they must reflect some varying environmental condition that influences growth of body and scales. The most obvious such element is temperature. Surface temperatures of the sea at several points along the coast have been compiled by the Scripps Institution of Oceanography, and have kindly been made available for this study by the Director, Dr. H. U. Sverdrup.
2/

Mean temperatures, at these points, for calendar years and for various combinations of months for years 1932 to 1938 inclusive, were averaged, and deviations computed in the same way as had been done with the growth increments. In all combinations of months tried, the deviations from the norm are negatively correlated with the anomalies in the calculated first year's growth. The means of temperatures measured at Scripps Institution Pier for the period June to August, however, had a higher negative correlation than those for other localities and other combinations of months; and deviations from their norm are shown inverted as the fifth curve of the series in figure 6. The months represented are those in which growth of young pilchards is most rapid (cf. Walford and Mosher, 1943).

Of more fundamental influence than the temperature on the marine environment, hence on biology of the pilchard, is wind. For it is the northwest winds prevailing along the California coast during spring and summer that produce the phenomenon of upwelling. This results in the transport of nutrients to the surface waters, making them available to the plankton organisms. Thus, ultimately, it results in the production of food which the pilchard eats.^{3/}

1/ The deviations given in the data collected in 1939-40 (top curve of fig. 6) are correlated with those corresponding in the data collected in 1940-41 (second curve of fig. 6), with an r of .93; and P of less than .01, according to Fisher's t test.

2/ Temperature data were studied for the following localities: Scripps Institution Pier at La Jolla, Lat. 32° 52' N.; the Pier at Balboa, Lat. 33° 36' N.; Hueneme, Lat. 34° 9' N.; Pacific Grove, Lat. 36° 38' N.; North Farallon Island, Lat. 37° 42' N.; Blunt's Reef, Lat. 40° 27' N.

3/ For a discussion of the relation between wind and the circulation along the Pacific coast, see Sverdrup, 1938.2, 1938.3; Sverdrup and Allen, 1939.

Lacking available records of offshore wind force, a series was derived from barometric pressure data given on daily weather maps published by the United States Weather Bureau (cf. Sverdrup, 1938.2). First were tabulated the daily barometric pressures at each of the four corners of a 300-mile square placed off the coast of southern California (cf. table 6). From these data were obtained two series of differences representing pressure gradients which would be expected to produce winds parallel and at right angles to the coast line, respectively; and their differences were summed by periods of time as described below.

The resulting two series of sums were treated, with due regard to the effect of the earth's rotation, as if they were components, the resultant of which is proportional to direction and extent of wind movement. The direction proved to be northwesterly for each period of the entire series studied.

Sums were made, as indicated above, for calendar years, and averaged for the period 1932-38, inclusive, to furnish a norm from which deviations were determined, as had been done with growth and temperature data, discussed above. The same procedure was followed using various periods of time and various combinations of months. Without exception the yearly deviations from normal indicated wind force were found to be correlated positively with anomalies in the first year's growth of pilchard. However, the period April through the following March gave a somewhat better correlation than other periods, and has been shown in the fourth curve of figure 6. This period corresponds with the first year's growth as registered on the scales: i.e., between the time of spawning and the time the first annulus is formed.

Other data bearing on the environment of the pilchard, made available by the Scripps Institution of Oceanography, are average monthly surface salinities for the same localities as cited in footnote 2, page 16. Those taken at the Scripps Institution pier were treated in the same way as described for the average monthly temperature records (page 16). Deviations from a norm based on the twelve-month period April to the following March - the same as that used for wind force - were plotted as the sixth curve of figure 6. This curve bears a strong similarity to the other five.

Thus is indicated a positive correlation between the force of northwest winds, the salinity of the surface water, and the first year's growth of pilchards; and a negative correlation between the latter and surface temperatures. To have demonstrated this required that the year classes, as determined from scales, be allocated correctly to the years in which they had been produced. It required also that a high enough order of accuracy be maintained in the scale reading to preserve the distinctive character of the curves.

A further conclusion to be drawn from these curves is that the fish of a given year class normally have a common history during their first year. They are subject to the same vicissitudes of marine climate and therefore probably also of food supply.

According to Lewis (1929), pilchards feed on diatoms and dinoflagellates, as well as upon copepods and other zooplankton. Moreover, the amount of food ingested is positively correlated with the abundance of surface plankton in the surrounding water. This in turn is controlled by temperatures; "low temperatures associated with upwelling of subsurface waters favor the growth of diatoms, which in turn attract the sardine" (Lewis, op. cit., p. 179). This being true, it is reasonable to expect growth in abundance of diatoms to favor growth of pilchards.

For study of this question, Dr. W. E. Allen has kindly made available statistics on relative diatom abundance, which he has observed for several years at the end of the Scripps Institution pier at La Jolla and at Heuneme.^{1/} Numbers of all species of diatoms per liter per week were summed by months; and the monthly totals summed in various groupings of months. No significant correlation between anomalies in these totals and anomalies in growth was found, no matter what grouping of months was used. However, the number of weeks in the year that the count of diatoms per liter exceeded 1,000, or 2,000 or 5,000, gave measures of diatom persistence, all of which showed a positive correlation with growth. As with the temperature and salinity data, these measures were summed by various combinations of months. The most satisfactory correlation was given by the number of weeks between June and the following May, inclusive, that the count exceeded 2,000 per liter. Deviations from the norm of that statistic taken over the period 1932-1938 are given in the seventh curve of figure 6. The period used, June through the following May, lags two months behind that used for wind data, and may indicate the time required for the action set up by the northwest winds to affect the supply of diatoms.

Although the abundance of diatoms thus appears to affect growth directly, it is a sustained abundance of these plants above a certain minimal level that is most effective in promoting growth, rather than sporadic flowerings of great abundance interspersed with periods of scarcity.

The relations between growth and other factors shown in figure 6 might not necessarily mean that pilchards normally spend the growing part of their first year of life near the locality where these data were collected. However, second and later growth increments were found not to be correlated with wind force, surface salinities, and temperatures measured at La Jolla. This may be explained in part by the fact that pilchards migrate successively greater distances as they grow larger, the extent of their migrations probably being a function of size more than of age. Consequently, the history of members of the same year class becomes less uniform as the fish grow older, though they probably never leave the Pacific coast save for seaward migrations of not more than 300 miles. This is all consistent with the conclusion that the bulk of pilchards in a year class do normally spend the first year of life in or near southern California, and that the subsequent history of the fish becomes so diverse that year-round conditions in any one locality can no longer reflect growth among the whole population of that year class.

^{1/} For the method of sampling, see Allen, 1936.

The most striking inconsistency in figure 6 is the lack of correlation for 1939 between growth on the one hand and diatom persistence and surface salinity on the other; also between surface temperature and surface salinity. Although the surface water at La Jolla was abnormally warm in 1939, it was also of abnormally high salinity; and though the diatom count was high, the average growth of fish of the year was below normal.

The breakdown of correlation between temperature and salinity suggests an important anomaly in the current pattern in 1939 in the vicinity of La Jolla. The relatively weak northwest winds prevalent that year are consistent with relatively weak upwelling; and the increase in salinity and temperature can indicate an increase in the admixture of "southern water" (cf. Sverdrup, 1938). The biological evidence of a change in hydrographic conditions is equally suggestive. Certain species of diatoms normally occurring several weeks of the year at La Jolla were absent in Dr. Allen's samples of 1939, notably, Chaetoceros curvisetus, Chaetoceros laciniosus, Licmophora lyngbyei, and Lithodesmium undulatum. Among species occurring more frequently in 1939 than normally, those most noteworthy were Rhizosolenia alata, Rhizosolenia fragilissima and Rhizosolenia imbricata. The ecology of these species is too little known to permit of interpreting their occurrence in terms of physical oceanography. It may be of significance, however, that among species of the first group mentioned above, all have been listed by Cupp and Allen (1938) as being south temperate neritic forms, except Licmophora lyngbyei, which is "tychopelagic". Among those listed in the second group, Rhizosolenia alata is an oceanic temperate form; and the other two are north temperate forms.

More direct evidence that a change in the environment of the pilchards took place in 1939 is the fact that an abnormally high production of young pilchards occurred that year in waters far to the north of southern California, which is regarded as the usual chief spawning ground. This may have been the result of abnormally high survival of young hatching from the number of eggs normally spawned north of California. It may also have been the result of abnormally heavy egg production in northern waters, permitted by a northward extension of oceanographic conditions favoring spawning. In support of the latter hypothesis is the fact that adult pilchards taken by fishermen in mid-summer off Oregon and Washington were full of spawn, in contrast to their usual immature condition at that time. That spawning actually occurred north of California is proved by the fact that the Fish and Wildlife Service that year collected pilchard eggs and larvae in tow nets off the Oregon coast (Walford and Mosher, 1941).

Whatever may account for it, an extraordinary number of young pilchards of year class 1939 were subsequently observed and caught from Oregon to Alaska, as well as along the California coast. It has been previously observed that the first year's growth decreases northward (Walford and Mosher 1943). Thus the northward extension of the range of year class 1939 could alone account for its abnormally low first year's growth in spite of the apparently favorable food supply in southern California.

SUMMARY AND CONCLUSIONS

Annual rings appear on the scales of adult pilchards, as in the young, and at the same time of year, namely, the winter and early spring. If the scales be properly prepared, these rings can be recognized and distinguished from false age marks by means of criteria set up in this study. The accuracy of following these criteria differs among readers and for different ages of fish being lower for older ages than for younger ones, but for the age distribution prevailing from 1939 to 1942, and for the persons reading the scales in this study, it averaged near to 93 percent.

The most important evidence supporting the validity of age determination by scales is that the fish allocated to each year class had growth characteristics in common, which appeared consistently in three seasons of sampling. These characteristics were expressed as the average first year's growth increment, calculated from scales. Departures of these averages from a norm were significantly correlated with anomalies in certain elements of the environment, thereby proving that the identification of the year classes had been correct.

The correlations indicated that, in general, growth during the first year is favored by a sustained presence of diatoms at optimum abundance. In turn, the latter is favored by upwelling, which is induced by northwest winds, and accompanied by low surface temperatures and high surface salinity, at least at the locality of observation.

In addition to an abnormally high first year of growth, year class 1938 was marked by having scales which averaged smaller than normal in relation to the length of the body.

No method has yet been devised of measuring the error of scale reading occasioned by the scales being irregularly marked; i.e., having too many or too few age rings. If this error were unduly high, however, specimens assigned to a given year-class would actually be composed of several ages; and if such mixing be complete, the average growth of the several year-classes should be uniform. In that event, the correlations referred to above would have become obliterated. The demonstration of the correlations, and their persistence for three seasons is evidence that the error was reasonably low, we judge, for the age composition prevailing, something of the order of ten percent or less. Thus, the relatively high accuracy of age determination of pilchards by scale reading--between 80 and 90 percent--and the fact that results are reproducible by different persons, warrants the confident utilization of this technique in the program of pilchard research.

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Figure 1. Left - A scale with 4 rings, the fourth close to the edge and touching it at the base of the sculptured portion.

Right - A scale with 4 rings, the fourth well within the edge.

Owing to their large size, irregular surface, and fine structure of the external folds, sardine scales do not photograph well.

In reading scales, it is necessary to focus continually, and sometimes to alter the lighting in order to see all parts of all rings. The following plates show ~~you what~~ what can be seen at a particular focus and lighting.

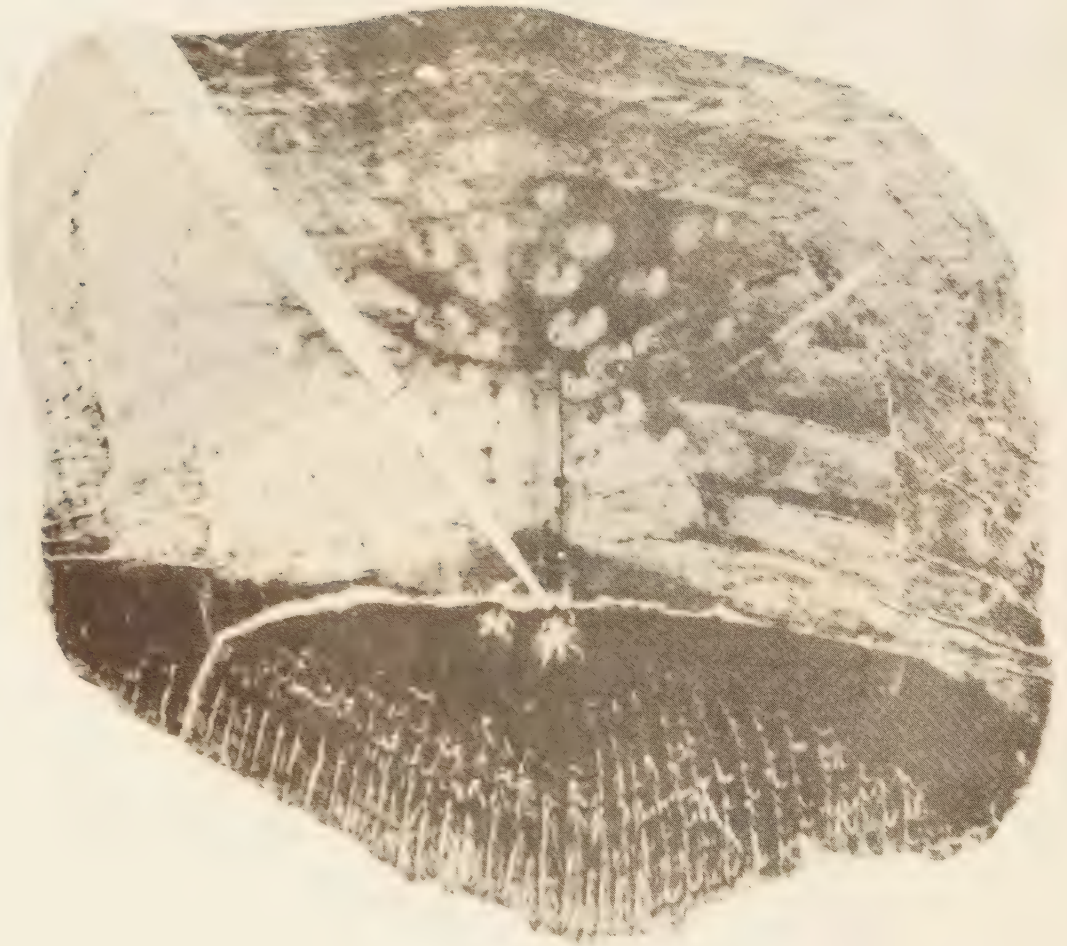


Figure 2. A pilchard scale with three rings, with a wide margin beyond the third ring.



Figure 3. A pilchard scale with 5 rings.

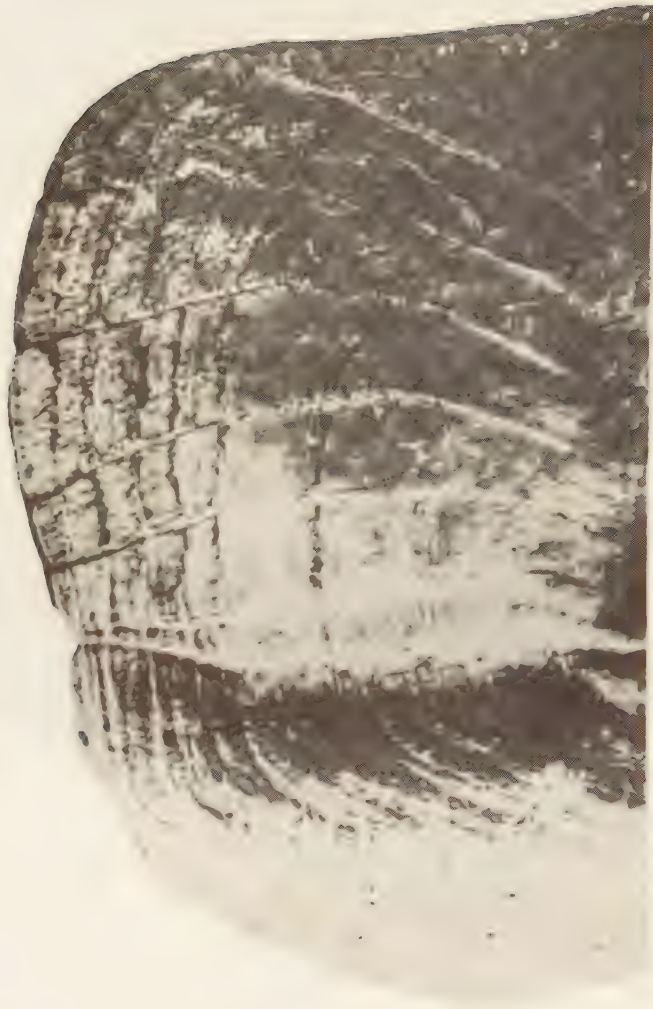


Figure 4. A pilchard scale with six rings.

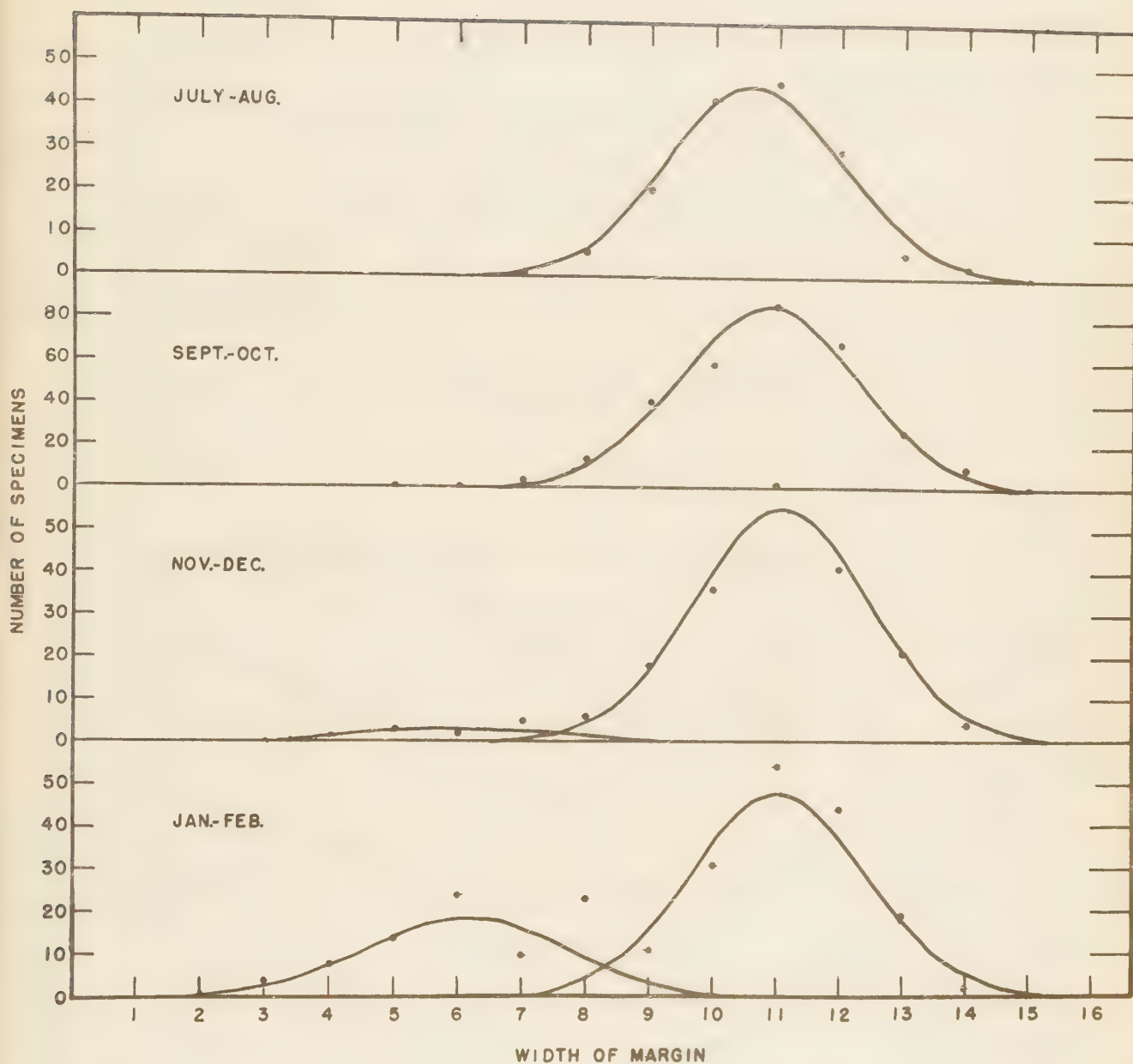


Figure 5. - Frequencies of widths of margin beyond last ring in scales having four rings. The data are fitted with normal curves to distinguish specimens having a recently formed annulus.

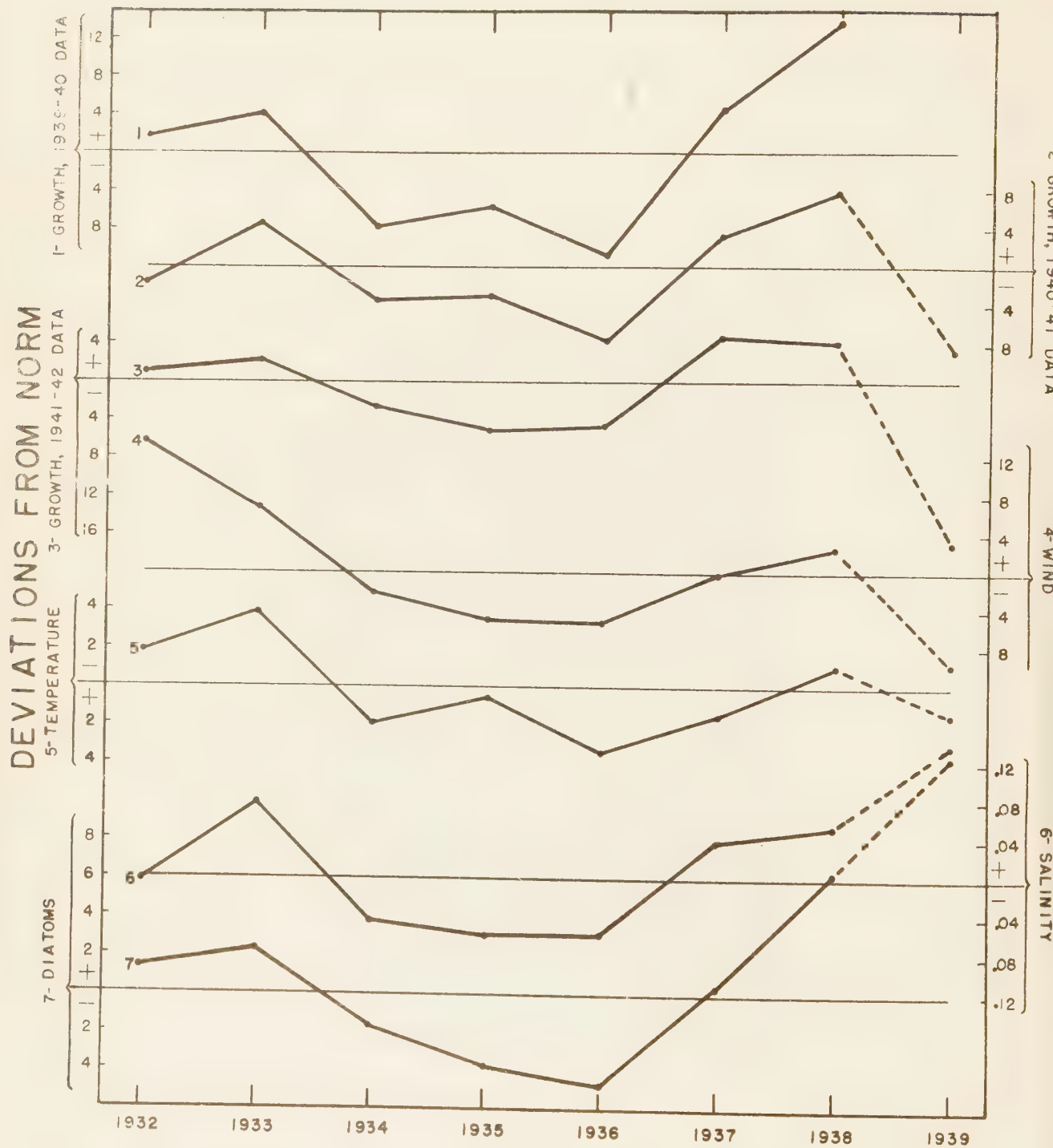


Figure 6. - Deviations from seven-year norm of growth in body length as computed from scales collected during three seasons, compared with similar deviations for various elements of the environment.

Table 5.- Frequencies of body lengths of pilchards at end of first year as calculated from scales

Body length	YEAR-CLASS											
	1932				1933				1934			
	Collected in season of				Collected in season of				Collected in season of			
	'39	'40	'41	'42	'39	'40	'41	'42	'39	'40	'41	'42
51-54	-	-	-	-	-	-	-	-	-	-	-	-
55-58	-	-	-	-	-	-	-	-	1	1	1	1
59-62	-	-	-	-	-	-	-	-	-	6	2	-
63-66	-	-	-	-	-	-	1	-	-	5	5	3
67-70	-	-	-	-	-	2	3	-	2	20	7	-
71-74	1	1	1	-	-	1	1	1	1	32	15	7
75-78	1	1	-	-	-	2	2	-	2	52	19	14
79-82	5	6	1	-	2	3	4	2	3	70	40	16
83-86	6	4	1	-	7	17	19	1	8	89	51	19
87-90	4	1	1	-	6	19	24	5	16	90	84	33
91-94	10	2	2	1	5	24	27	2	18	67	67	31
95-98	10	13	7	1	10	27	20	7	24	76	90	59
99-102	16	7	7	1	19	17	24	4	29	64	87	40
103-106	9	4	4	1	17	24	21	1	22	36	84	34
107-110	11	4	4	1	24	20	27	9	40	49	90	37
111-114	11	5	5	1	20	14	10	7	30	28	66	22
115-118	15	5	5	1	18	17	13	3	26	27	47	26
119-122	11	2	2	-	17	13	9	1	19	20	53	15
123-126	7	4	3	1	13	12	6	1	11	24	42	10
127-130	6	3	3	1	12	7	10	1	10	11	18	11
131-134	9	-	-	-	9	7	7	-	5	8	11	7
135-138	3	2	2	-	11	6	3	1	4	2	6	6
139-142	3	3	2	-	6	6	2	3	2	3	3	4
143-146	8	3	2	-	1	4	2	1	4	2	2	1
147-150	3	1	1	-	1	4	2	1	1	1	1	1
151-154	1	-	-	-	-	-	-	-	1	-	-	-
155-158	-	-	-	-	-	-	-	-	-	-	-	-
159-162	-	-	-	-	-	-	-	-	-	-	-	-
Totals	150	60	92	27	251	209	53	99	294	320	906	377

1/ Figures are not adjusted to take into account departures from exact proportionality of scale length to body length.

Table 5 (Cont'd.) Frequencies of body lengths of pilchards at end of first year as calculated from scales

Body length	YEAR-CLASS					
	1937		1938		1939	
	Collected in season of		Collected in season of		Collected in season of	
	'39- '40	'40- '41	'39- '40	'40- '41	'40- '41	'41- '42
51-54	-	-	-	-	-	-
55-58	-	-	-	-	-	-
59-62	-	1	-	-	1	-
63-66	-	1	-	-	3	-
67-70	-	2	-	1	29	-
71-74	-	3	-	1	69	1
75-78	1	2	-	6	147	-
79-82	5	11	-	4	242	-
83-86	8	7	-	14	365	-
87-90	14	19	-	27	442	2
91-94	23	37	2	37	542	2
95-98	38	32	9	59	559	5
99-102	53	55	12	68	490	6
103-106	87	82	34	78	41	11
107-110	106	144	35	92	405	17
111-114	146	145	54	94	304	32
115-118	129	147	66	78	216	38
119-122	147	177	93	73	119	68
123-126	122	157	74	73	75	66
127-130	102	119	86	71	30	59
131-134	91	93	62	38	15	40
135-138	76	58	59	32	8	37
139-142	36	39	26	18	10	25
143-146	11	27	13	8	4	9
147-150	5	4	9	4	3	6
151-154	4	1	3	-	2	3
155-158	-	-	-	-	-	1
159-162	-	-	-	-	-	-
Totals	1205	1376	637	876	325	428
					4093	

Table 5 (Cont'd.) Frequencies of body lengths of pilchards at end of first year and calculated from scales

YEAR-CLASS												
1932			1933			1934			1935		1936	
Collected			Collected			Collected			Collected			
in season of			in season of			in season of			in season of			
by			by			by			by			
Districts			Districts			Districts			Districts			
California												
S. P.			-			-			-			
Mont.			12			44			6			
S. F.			17			35			114			
Oregon			6			17			18			
Washington			138			207			110			
Brit. Col.			25			109			101			
YEAR-CLASS												
1937			1938			1939			1940			
Collected			Collected			Collected			Collected			
in season of			in season of			in season of			in season of			
by			by			by			by			
Districts			Districts			Districts			Districts			
California												
S. P.			99			763			178			
Mont.			1205			737			211			
S. F.			1288			590			9			
Oregon			20			51			6			
Washington			43			101			19			
Brit. Col.			25			125			5			
1/ San Pedro												
2/ Monterey												
3/ San Francisco												

Table 6. - The symbols "a", "b", "c", "d" refer to the four corners of the square, mentioned on page 29, for which barometric pressures (in inches of mercury) A, B, C, D, respectively, were calculated by interpolation between isobars on daily weather maps. The figures given are monthly sums of these daily interpolations. The points are located approximately as follows:

a, lat. $32^{\circ} 26'$ N.; long. $126^{\circ} 12'$ W.; b, lat. $35^{\circ} 16'$ N., long. $121^{\circ} 15'$ W.; c, lat. $30^{\circ} 58'$ N.; long. $118^{\circ} 28'$ W.; d, lat. $28^{\circ} 16'$ N.; long. $123^{\circ} 17'$ W.

They are so placed that $(A+D) - (B+C)$ will give a pressure gradient in a direction from which one would infer a wind parallel to the coast line, assuming deflection to be 73 degrees. Similarly, the difference between $(A+B)$ and $(C+D)$ would give a pressure gradient from which a wind at right angles to the coast would be inferred. For the study discussed in this paper, the aforesaid differences were computed from twelve-month summations of the monthly sums of daily pressures. They were treated as components, and converted to their corresponding resultants (R) with the following formula:

$$R = \sqrt{[(A+D) - (B+C)]^2 + [(A+B) - (C+D)]^2}$$

Table 6 (Cont'd.)

	1932				1933				1934			
	A	B	C	D	A	B	C	D	A	B	C	D
Jan.	937.503	934.254	933.481	935.456	936.599	931.748	930.689	931.831	937.989	935.982	933.025	934.720
Feb.	872.162	870.575	870.115	871.226	847.543	845.450	842.827	844.598	841.877	842.868	842.739	842.727
Mar.	935.457	932.554	930.931	932.860	934.889	932.997	931.767	934.214	934.818	932.747	931.110	933.473
Apr.	903.458	900.785	899.648	902.056	904.809	900.820	899.772	902.958	902.926	900.254	898.987	901.690
May	933.356	929.833	929.274	931.993	935.294	931.828	930.781	934.099	933.085	929.577	928.531	931.759
June	901.243	897.184	896.647	899.491	902.986	899.557	899.134	901.782	902.355	898.807	898.438	901.479
July	932.459	927.924	927.714	930.151	932.418	927.435	926.944	930.344	932.737	929.228	928.750	931.359
Aug.	930.615	926.625	926.515	929.183	931.178	927.601	926.658	929.485	932.116	929.201	928.427	930.414
Sept	902.014	897.695	897.453	899.736	901.148	896.811	896.610	899.534	901.107	896.614	896.803	899.179
Oct.	932.610	929.759	928.143	930.032	932.061	929.572	928.537	930.611	931.310	930.672	929.244	930.772
Nov.	903.554	902.464	900.409	901.978	905.609	903.612	900.927	903.324	903.722	902.914	900.980	903.052
Dec.	934.674	933.557	931.511	932.749	933.464	933.721	932.901	933.401	935.011	933.956	931.083	932.310
	1935				1936				1937			
	A	B	C	D	A	B	C	D	A	B	C	D
Jan.	931.398	932.337	930.863	931.153	932.973	932.717	930.934	931.927	934.359	932.691	931.962	933.671
Feb.	844.492	843.874	841.610	842.687	871.477	870.642	870.490	870.988	842.571	842.133	841.968	843.208
Mar.	934.203	931.849	931.368	933.275	932.155	929.979	929.129	930.383	931.145	929.812	929.318	930.714
Apr.	900.938	899.524	899.365	901.583	903.470	902.235	901.782	902.768	905.072	902.505	900.420	903.218
May	932.979	928.799	928.299	931.281	932.030	929.008	927.071	931.145	932.734	928.343	927.707	931.072
June	902.639	897.958	897.884	901.382	900.523	897.752	897.061	893.881	901.376	898.911	898.248	900.630
July	932.253	928.568	927.965	929.878	931.013	926.946	926.699	929.158	932.191	928.394	926.672	930.515
Aug.	929.238	926.548	925.131	926.838	931.428	927.665	927.031	929.545	931.809	928.538	927.672	929.804
Sept.	900.191	898.185	896.985	898.931	899.533	896.319	895.910	898.179	901.258	898.041	896.903	899.360
Oct.	932.282	930.607	928.907	930.704	931.466	929.075	928.161	930.087	931.453	929.501	928.297	930.648
Nov.	904.224	902.459	901.311	902.378	903.985	903.471	900.497	900.915	904.567	902.162	901.390	903.146
Dec.	932.625	932.188	930.741	931.882	933.114	931.756	930.535	931.322	932.535	932.482	930.623	931.305
	1938				1939				1940			
	A	B	C	D	A	B	C	D	A	B	C	D
Jan.	935.436	934.033	931.389	933.660	935.803	932.795	931.016	934.159	931.006	931.936	932.132	932.694
Feb.	840.539	840.935	841.403	841.709	847.656	844.378	842.861	845.337	872.077	872.173	872.340	872.401
Mar.	931.252	931.167	930.817	932.559	935.508	932.832	932.446	934.484	933.038	931.453	930.551	932.067
Apr.	904.124	901.164	900.116	903.103	904.325	901.264	900.645	902.687				
May.	933.012	929.655	928.714	931.683	932.814	928.755	929.182	932.076				
June	901.903	898.261	897.768	899.231	902.166	898.535	897.907	900.280				
July	932.067	929.119	929.036	930.787	932.526	928.865	928.340	931.167				
Aug.	931.276	928.148	927.785	929.887	931.086	928.647	928.049	929.766				

1938

	1938				1939			
	A	B	C	D	A	B	C	D
Sept.	899.150	897.725	897.209	898.932	899.929	897.328	896.329	898.018
Oct.	932.071	929.812	930.184	931.277	933.200	930.857	929.658	931.459
Nov.	904.716	903.350	901.035	902.435	904.560	902.551	900.911	903.103
Dec.	933.773	932.562	931.487	932.633	934.361	933.728	932.614	934.380

Table 7.—Average monthly surface temperatures in degrees centigrade at Scripps Institution Pier, La Jolla, California. Recorded by Scripps Institution of Oceanography.

YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1932	13.28	13.27	14.80	14.81	16.08	18.99	19.49	18.75	18.62	17.40	16.18	14.00
1933	13.01	12.60	13.46	14.90	15.39	17.27	18.65	19.04	16.96	17.22	15.42	13.91
1934	13.27	13.95	15.74	17.32	19.21	19.06	20.47	20.47	20.55	17.87	16.96	15.46
1935	14.39	14.05	13.26	15.04	17.59	18.87	19.98	20.74	19.36	17.19	15.29	14.76
1936	13.97	14.64	15.11	14.24	18.08	17.96	22.35	22.08	20.95	18.57	17.28	16.10
1937	13.43	13.13	14.25	14.90	17.71	19.11	20.76	20.63	20.58	17.73	16.97	15.30
1938	15.01	14.39	14.59	15.12	16.71	17.84	19.07	20.98	20.06	17.05	14.52	14.78
1939	14.08	11.96	13.21	15.53	16.68	18.36	20.69	21.31	19.45	19.23	18.17	17.43
1940	15.84	15.19	15.05	16.47	18.60	18.16	18.34	20.63	19.22	18.62	16.03	16.11

Table 8.--Average monthly surface salinity ^{1/} at the Scripps Institution Pier, La Jolla, California. Recorded by Scripps Institution of Oceanography

YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1932	.64	.21	.39	.62	.67	.69	.68	.59	.56	.49	.57	.53
1933	.49	.45	.54	.58	.69	.80	.77	.76	.66	.68	.68	.62
1934	.54	.53	.53	.61	.67	.68	.68	.58	.61	.52	.52	.43
1935	.40	.28	.42	.51	.60	.65	.62	.59	.51	.50	.49	.54
1936	.51	.26	.46	.58	.64	.67	.75	.72	.66	.45	.55	.52
1937	.40	.25	.04	.37	.57	.68	.72	.75	.76	.67	.71	.62
1938	.70	.66	.15	.66	.73	.78	.79	.75	.65	.56	.57	.53
1939	.48	.49	.57	.61	.75	.81	.86	.82	.62	.68	.72	.76
1940	.72	.60	.63	.58	.71	.70	.64	.71	.57	.52	.44	.37

Figures given are minus 33.00; i.e., add 33.00 to obtain actual salinities.

1/

Table 9.--Number of weeks^{1/}, by months, that counts of diatom cells, as sampled by W. E. Allen^{2/}, at the Scripps Pier, La Jolla, were of various categories of magnitude

YEAR	DIATOM COUNT	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1932	499 or less	-	-	3	-	-	-	-	1	1	4	-	1
	500 -- 999	-	1	-	-	-	-	3	2	-	-	2	-
	1,000 -- 1,999	2	-	-	-	-	-	1	-	1	1	2	-
	2,000 & more	2	4	1	4	5	4	-	2	2	-	-	3
1933	499 or less	-	-	-	-	-	1	-	-	1	-	-	-
	500 -- 999	-	-	-	-	-	2	1	2	1	-	-	-
	1,000 -- 1,999	1	1	-	-	-	-	-	-	1	1	1	1
	2,000 & more	3	3	5	4	5	1	3	3	1	3	3	4
1934	499 or less	-	-	3	-	-	-	1	-	2	2	1	2
	500 -- 999	-	-	1	-	1	-	1	1	1	-	-	1
	1,000 -- 1,999	2	-	-	-	-	-	2	3	-	1	1	-
	2,000 & more	2	4	1	4	4	4	-	1	1	1	3	1
1935	499 or less	1	-	-	-	1	-	-	-	-	1	1	-
	500 -- 999	1	-	-	-	2	1	-	2	-	1	3	2
	1,000 -- 1,999	-	1	-	-	-	-	-	-	2	-	1	1
	2,000 & more	2	3	5	4	1	2	4	3	2	2	-	1
1936	499 or less	-	2	1	-	4	-	-	-	2	1	2	3
	500 -- 999	-	1	-	-	1	1	-	-	2	-	1	1
	1,000 -- 1,999	2	1	2	1	-	-	-	1	-	3	1	1
	2,000 & more	2	1	1	3	-	3	4	4	-	-	-	-
1937	499 or less	-	2	1	-	-	-	1	1	-	2	-	1
	500 -- 999	-	-	1	-	2	1	2	2	-	1	2	1
	1,000 -- 1,999	1	-	-	-	2	-	-	-	1	-	2	1
	2,000 & more	3	2	3	4	1	3	1	2	3	1	1	1
1938	499 or less	1	-	-	-	-	-	-	-	-	1	-	4
	500 -- 999	-	-	-	-	-	-	-	-	-	-	-	1
	1,000 -- 1,999	2	-	2	1	-	1	-	2	-	-	-	1
	2,000 & more	1	4	3	3	5	3	4	3	4	3	4	-
1939	499 or less	-	-	1	-	-	-	-	1	-	-	-	-
	500 -- 999	1	-	1	-	-	-	-	1	-	-	-	-
	1,000 -- 1,999	2	-	1	-	-	1	-	1	-	-	-	3
	2,000 & more	1	4	2	4	5	3	4	1	5	4	5	1
1940	499 or less	-	-	-	-	-	-	-	-	-	-	-	1
	500 -- 999	1	1	1	1	-	-	-	-	-	1	-	1
	1,000 -- 1,999	-	1	1	1	-	-	-	-	1	1	-	1
	2,000 & more	3	4	3	3	5	4	4	5	3	3	4	1

1/ A week divided between two months was assigned to whichever one of them included most of its days.

2/ Cf Allen, 1936, for method of sampling.

4. Influence of Temperature on the Rate of Development of Pilchard Eggs in Nature.

By

Elbert H. Ahlstrom 1/

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INTRODUCTION

In the first paper of this series^{1/}, Sette, 1943, has stated that a major requisite in the program of pilchard research is the measurement of recruitment. This can be obtained most directly from a quantitative sampling of pilchard eggs and larvae at sea in and around the region known to be the chief spawning grounds. Determinations of the amount of spawning require the integration (over both time and space) of the quantitative samples of eggs. To accomplish this necessitates knowing as exactly as possible the age of any particular stage of development, as well as the number of days of spawning represented in each collection. Since rate of development is strongly influenced by temperature, it is necessary to know the relation between these two variables to get a precise method of determining the age of eggs in all samples.

So far it has been unfeasible to procure live spawning pilchards for artificial fertilization and propagation of eggs. Fishermen rarely catch ripe, spawning pilchards, and we have lacked facilities wherewith we could attempt to catch them. Although eggs newly spawned were collected in the plankton samples, constant temperature apparatus was not available to permit hatching experiments under controlled conditions. Hence, it has been necessary to approach the problem analytically by correlating temperature data collected in the field with the probable length of time particular stages in the samples had been developing.

The writer is indebted to Oscar Elton Sette, in charge of the South Pacific Investigations, for continuous aid and advice throughout the development of this problem, to Dr. L. A. Walford for valuable help in the preparation of the manuscript, and to Elizabeth Vaughan for assistance and suggestions in the mathematical treatment. The plankton hauls for the most part were made by the author and other members of the South Pacific Fishery Investigation staff of the Service, while the oceanographic observations, of which the temperatures-data of this paper were a part, were the responsibility of the Scripps Institution of Oceanography staff. Sorting of the plankton collections was accomplished with the assistance of employees from Works Progress Administration projects Nos. 10917 and 65 - 2 - 08 - 286.

COLLECTION OF MATERIAL

The plankton collections on which this paper is based were made during the pilchard spawning surveys of 1940 and 1941, conducted by the South Pacific Investigations of the Fish and Wildlife Service in conjunction with the Scripps Institution of Oceanography from the research

^{1/}Oscar Elton Sette. Studies on the Pacific Pilchard or Sardine (*Sardinops caerulea*). I - Structure of a Program for Pacific Pilchard (or Sardine) Research. Special Scientific Report No. 19.

essel, E. W. Scripps. Six cruises, each covering a pattern of approximately forty stations, were made during the spring and early summer of each year. The region surveyed is the area of maximum spawning of the pilchard (Seefield, 1934). It had as its northern limit the group of islands of which Santa Cruz is the largest, and extended in the south to near the Coronados Islands; the stations ranged from near shore to about 150 miles out to sea. The region covered and the pattern of stations occupied was somewhat different during the second season, but essentially the same area was surveyed in both years.

The methods employed in the collection of plankton samples containing pilchard eggs will be treated in detail in another paper devoted to the results of the spawning surveys of the years 1940 and 1941. For the purposes of the present article, it is sufficient to state that oblique hauls were made with either a one-meter or two-meter net from approximately 75 meters deep to the surface, the hauls taking, on the average, about 24 minutes of towing time. Stations were occupied at whatever hour of the day or night they were reached. Temperatures were taken at each station at 10-meter intervals in the upper 50 meters of water and at 25-meter intervals in the next 50 meters, with reversing thermometers attached in pairs to Nansen water bottles.

DESCRIPTION OF THE PILCHARD EGG

The pilchard egg can be readily identified by the following combination of characters: a wide perivitelline space, a single oil globule, and an irregularly segmented yolk. The eggs are spherical, with the egg membrane thin, unsculptured, quite transparent, and with a bluish or purplish cast. The egg membrane is easily broken, more so than those of most planktonic eggs; in the plankton samples studied it was commonly absent from a third to a half of the eggs, probably having been broken in the net, or in fractioning or sorting the material. Fertilized eggs average about 1.70 mm. in diameter (range 1.35 - 2.05 mm.). This is of similar size to the fertilized egg of the European pilchard. The perivitelline space is wide, having nearly as great a width as the yolk mass. We have encountered no other pelagic fish egg of the size of the pilchard egg in the area investigated that are so characterized. The yellowish-brown yolk appears to be made up of a number of irregular cells, but it is composed of a large number of separate particles of yolk material closely pressed together. There is a single oil globule, 0.16 mm. in diameter.

In connection with these studies the development of the pilchard egg was separated, on the basis of readily observable morphological character, into eleven stages which are not of equal time duration. A brief description of each stage is given in the appendix (p. 9).

TIME OF SPAWNING

As there are no actual observations on the time of day pilchards spawn in nature, this could be determined only by indirect evidence. The time of day newly-spawned eggs appear in the plankton should roughly establish the time of spawning. Such newly-spawned eggs would be pre-cleavage eggs that had not had time to begin cell division, i.e., stage I (cf. appendix). The times when pre-cleavage eggs occurred in plankton samples is summarized in tables 1 and 2. According to both tables about 87 percent of pre-cleavage eggs were taken during the four-hour period, 8:00 p.m. to midnight. At that time there were practically no eggs in the early stages of cleavage. After midnight very many pilchard eggs undergoing cleavage were in the samples taken, while only an occasional egg was of precleavage stage.

Eggs of that age taken during the four-hour period before midnight are considerably smaller in diameter than are those with some embryonic development. Since the yolks are of similar size in both groups, the difference lies in the width of the perivitelline space, which is nearly wanting in pre-cleavage eggs taken during this period; such eggs averaged only 1.20 mm. in diameter (range 1.02 - 1.38 mm.). This is slightly smaller than the average size of 1.24 mm. that F. N. Clark (1934, p. 3) reported for mature pilchard eggs from ripe females. The difference in size between eggs newly-spawned and those undergoing development (average size 1.70 mm.) could result from the latter having absorbed water, swelling the perivitelline space up to the size characteristic of planktonic pilchard eggs.

A few pre-cleavage eggs were taken in the samples after midnight. The majority of these were much larger than pre-cleavage eggs taken before midnight (cf. tables 1 and 2), in fact, were about the same size as pilchard eggs in the same samples undergoing cleavage. Hence, they must have been in the water for some time, and, consequently, must either have started development very slowly or had remained unfertilized. However, a few pre-cleavage eggs taken as late as mid-day have a very narrow perivitelline space. Either these had been spawned at the normal time but did not attain the typical planktonic egg size, or they resulted from isolated instances of deposition during the day. In numbers such eggs were negligibly few.

Further support for the thesis that spawning is rhythmical, occurring during a brief, relatively fixed time each day and not sporadically, is furnished by the time distributions of eggs undergoing cleavage. Thus, eggs in early stages of cleavage were taken immediately after midnight and not during any other period of the day, while eggs in the last stages of cleavage were collected in samples around noon. This could occur only if spawning took place during a brief period each day.

The following account of the length of time of development assumes that spawning is confined to the period, 8:00 p.m. to midnight, by taking the midpoint of this period, 10:00 p.m., as the hour when development is initiated. True, using the time of fertilization rather than of spawning would be more precise, but the two processes are believed to occur close enough together to justify neglecting the time difference between them.

Table 1.--Samples in which pre-cleavage eggs were taken

(Regular survey cruises of 1940-1941)

Station No.	Time of collection ^{1/}	Number of pre- cleavage eggs ^{2/}	Number of stage II eggs	Number of stage III and stage IV eggs	Av. size pre- cleavage eggs
1744	20:16	41	-	-	1.21 mm.
1752	20:34	11	-	-	1.22 "
1736	21:15	12	-	-	1.19 "
2135	21:20	22	-	-	1.15 "
1751	21:48	4	-	-	-
1731	21:53	79	1	-	1.07 "
112	22:17	15	-	-	1.31 "
105	22:30	6	-	-	1.35 "
1952	23:33	4	-	-	1.20 "
2115	23:37	100 ^{3/}	-	-	1.20 "
1745	1:02	1	2	-	-
1926	2:24	1	38	-	-
1915	2:47	1	30	-	1.60 "
336	4:00	1	75	-	-
128	5:45	1	13	-	1.78 "
1714	6:47	1	433	-	-
2325	6:58	1	156	-	1.05 "
1743	7:49	4	808	-	1.04; 1.70 mm. ^{4/}
411	8:05	1	46	-	-
414	8:27	1	307	-	-
1955	8:35	3	225	-	-
405	9:30	1	14	-	1.60 mm.
1946	10:32	2	5	-	1.54 "
2324	10:36	3	19	-	-
1715	10:53	1	14	2	-
114	11:00	2	7	1522	-
132	11:15	1	-	60	1.65 "
1742	12:10	1	1	80	-
2113	12:27	8	523	196	-
409	12:45	1	103	1	-
2163	12:47	1	-	193	1.04 "
330	13:03	2	116	15	-
124	15:17	1	-	67	-
1726	17:25	1	-	18	-

^{1/} The time of collection as used in tables 1 and 2 refers to the time when the plankton net was going through the 20-10 M. zone.

^{2/} Number of eggs in the sorted portions of all nets used at a station, whether of 2 M, 1 M, or 1/2 M diameter.

^{3/} Approximate number.

^{4/} Eggs of two size groups.

Table 2.--Pre-cleavage eggs in samples of transection^{1/}

Station No.	Time of collection	Number of pre-cleavage eggs	Number of stage II eggs	Number of stage III eggs	Average size pre-cleavage eggs
1876	19:00	-	-	-	-
1877	20:06	26	-	-	1.07 mm.
1878	21:06	112	-	-	1.13 "
1879	22:08	91	2	-	1.28 "
1880	23:11	68	12	-	1.32 "
1881	00:13	3	57	-	-
1882	1:12	5	330	-	-
1883	2:23	4	1198	-	-
1884	3:27	5	1088	-	-
1885	4:34	9	2157	-	1.68 "
1886	5:22	10	2347	-	-
1887	6:30	2	1136	195	-
1888	7:30	2	156	806	-

^{1/} This table is based on collections from a special series of stations occupied on the night of April 8-9, 1941, when stations were taken on a line extending from off the southern end of San Clemente Island toward the mainland at 2.5- to 5.0-mile intervals, with about an hour's time elapsing between successive samples. Fortunately, this series of samples was obtained from a region where heavy spawning was taking place the night of collection.

DURATION OF DEVELOPMENT

The length of time required by pilchard eggs to develop to the hatching stage after being spawned and fertilized was roughly determined by placing pilchard eggs taken in plankton samples into hatching jars aboard the vessel while at sea and following their development. This was done during several cruises in 1940. In some samples the development of eggs was followed from the blastodermal cap stage to hatching. From these experiments, it was concluded that the pilchard egg ordinarily required about three days to develop to the hatching stage from the time of spawning. Because the temperature of the hatching-jars could not be kept constant with the facilities available at sea, it fluctuated several degrees during each twenty-four hour period. Hence, the data derived from these experiments is not of direct use in the study of the influence of temperature on the rate of development.

Since the pilchard egg is spawned only during a few hours of the twenty-four (8:00 p.m. to midnight), and since it requires several days for the process of development, a plankton sample should contain eggs in various stages of development; furthermore, there should be a sharp separation of the stages among eggs derived from each day's spawning. A tabulation of the stages of development present in the samples (table 6) reveals that a sample typically contains stages in various degrees of development separated by gaps of one or two stages, which are taken to represent the time gaps between successive spawnings. Thus, we have a basis for separating the stages present in a sample into their respective days of spawning^{2/}; with the least advanced stage (or stages) taken to represent the most recent spawning, and so on. In some samples one or more days of spawning may not be represented, but this can usually be ascertained by a comparison with other samples. As a consequence, there are often insufficient landmarks to indicate the age of such stages as are present.

Having effected a separation of the eggs in a plankton sample into their respective days of spawning, the actual time of development of each stage present in a sample can be determined. The midpoint of spawning, 10:00 p.m., is taken as the hour when development commenced. The time of preservation of each plankton sample marks the endpoint of development of the eggs present in the sample, and this time was recorded as a part of the routine observations during collection of the material. From these data it is possible to derive the probable length of time, in hours, that each of the several stages in most samples had been developing.

WATER TEMPERATURES

In correlating the development of pilchard eggs with the temperature of the water at the station of collection, it is necessary to express the

^{2/} Separation into days is indicated for each sample listed in table 6.

temperature at each station by a single value. For that purpose the average of the temperatures at 10 and 20 meters was used.^{3/} This choice was based on the results of a series of horizontal hauls made with closing nets (cf. Silliman, 1943), which showed that although a few pilchard eggs are occasionally found deeper than 50 meters, nearly all occur above 30 meters, and by far the greatest concentration is usually between 10 and 20 meters or even nearer to the surface. Surface temperatures, however, were not included in the average, because of their rather marked fluctuations.

To be sure, the temperature readings may not represent exactly the average temperature to which the eggs had been subjected from spawning to the time of collection. However, we can assume, relatively safely, that the temperature of the sea water usually had not changed very much during this period of time, which, on the average, would have been only about a day and a half.

Pilchard eggs were found developing at temperatures ranging from 12.5° C. to 17.6° C. as measured by the mean of the 10 - 20 meter levels; this is an over-all range of slightly more than 5.0° C. However, the majority of samples containing pilchard eggs were taken at temperatures between 13.5° C. and 16.0° C., or within a range of 2.5° C.

INFLUENCE OF TEMPERATURE ON RATE OF DEVELOPMENT OF PILCHARD EGGS

The primary information upon which the analysis of the relation between temperature and rate of development of pilchard eggs in nature can be made are the following: (1) The estimated age, in hours, of most pilchard eggs from the time of spawning to the time of collection and (2) the temperature of the water at the depths where the majority of eggs were developing, taken at the time of collection of the eggs.

An analysis could not be made of the influence of temperature on the length of time required by the pilchard egg to develop completely to hatching, because of the difficulty of determining, from the preserved material, when hatching would have occurred. However, a correlation was possible between temperature and length of time of development of the pilchard egg to the stage immediately preceding hatching (stage XI, cf. appendix).

Not all records of stage XI could be used in the correlation, since, in some samples, only a small percentage of the eggs referred to a common day of spawning had reached this stage, the majority still being in the preceding stage; also, in a few samples the age of the eggs could not be determined with certainty. Therefore, the following criteria were set

^{3/} Temperatures at 10 and 20 meters were usually closely similar, and both depth usually occurred in the stratum above the thermocline. For more than 50 percent of the items used in the subsequent correlations, the difference in temperature between these two depths was less than 0.1° C., and for only one-sixth of the items was the difference greater than 0.5° C.

up to select' the records of stage XI to be used in the analysis: (1) At least four-fifths of the pilchard eggs of a given day's spawning must have reached the stage, (2) there must be at least two specimens of the stage in each included record, and (3) there must be a reasonable certainty about the length of time of development, based on evidence of associated stages of development.^{4/}

When the length of time of development of each record of stage XI meeting the criteria was plotted as the dependent variable against the temperature of the water at the station of collection, a scatter of points was obtained that apparently could be fitted best by a curved line. By using the logarithm of the time of development for plotting against the temperature of the water a straight line distribution resulted (uppermost curve in figure 1), which was subsequently fitted by the method of least squares.

A similar correlation of temperature with length of time of development was also made on three-earlier stages of pilchard eggs, III, VI, VIII-IX (combined to give more items)^{5/} The fitted lines for these stages, also shown in figure 1, have about the same slope as the fitted line for stage XI. In fact, when tested statistically, the four lines were not significantly different from each other ($P > .05$). The slopes are defined by the b values in the equation $Y = a + bX$; these values are listed in table 3, together with other pertinent data concerning the correlations. There is no evidence that the relation between temperature and rate of development changed during incubation. Furthermore, the results obtained for the four stages are so consistent that they justify confidence in the reliability of the method of analysis. The time (in hours after spawning) to reach each of the four stages at temperatures between 13.5 and 17.0° C. is given by 0.5 degree intervals in table 4. Within the temperature range investigated, the time to reach a stage of development is increased by about 7.15 percent for each 0.5° C. decrease in temperature. The total time of development to hatching, could be approximated by adding two to three hours time to the values listed for stage XI at the higher temperatures, and proportionately more as the temperature decreases.

Although consistent results are obtained for the several stages, there is a considerable spread of points about each line. The factors causing this variability may be associated with either the time of development or with the temperature. Variable elements associated with time undoubtedly account for most of the spread about the four fitted

^{4/} The records of stage XI meeting the above criteria are indicated in table 6 by an asterisk.

^{5/} All records of these stages that could meet the three criteria previously described for stage XI were used in the correlations; these are indicated in table 6 by an asterisk.

FIGURE 1

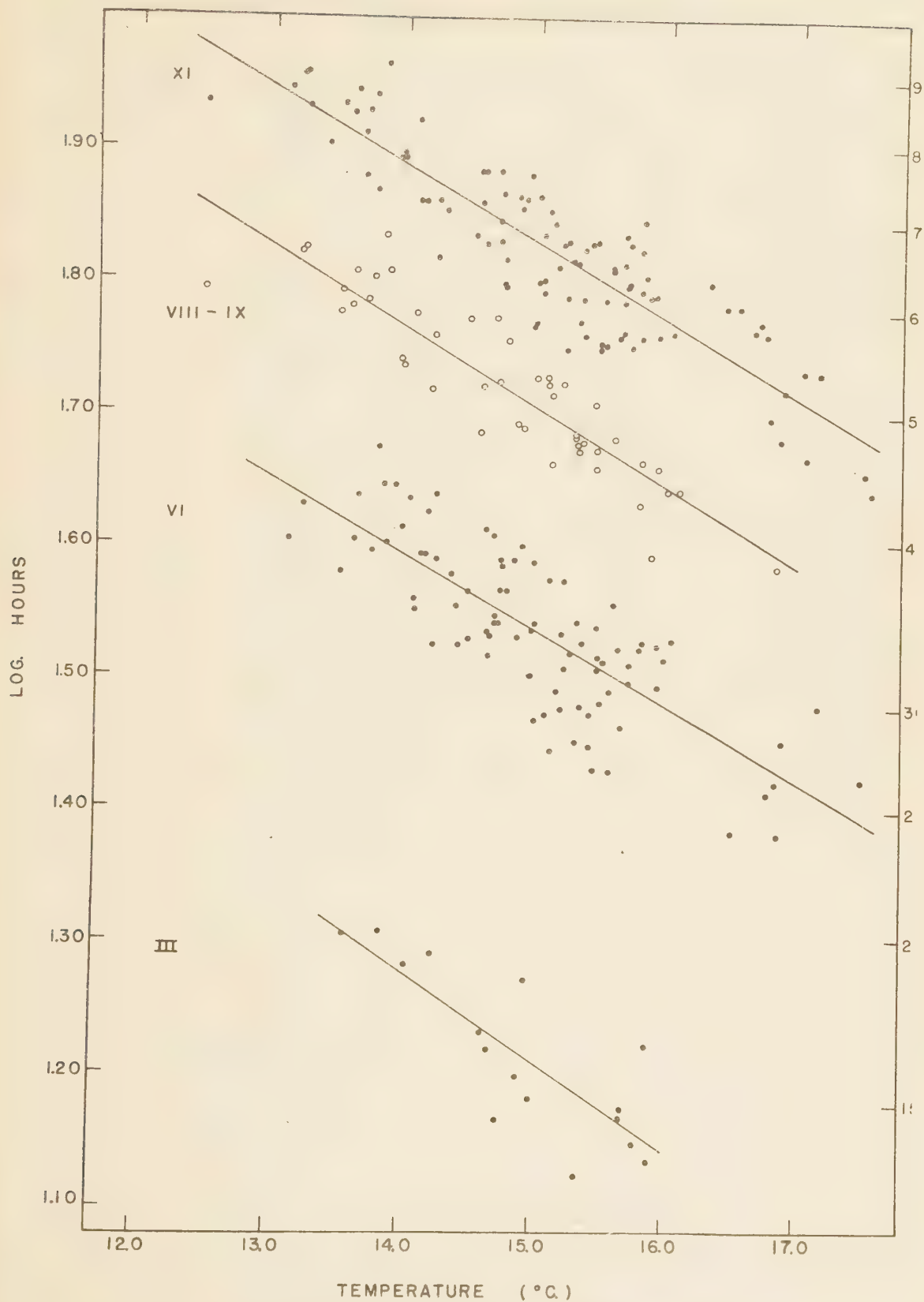


FIGURE 1. - REGRESSION DIAGRAM SHOWING THE INFLUENCE OF TEMPERATURE (°C) ON THE TIME OF DEVELOPMENT (LOG. HOURS) OF PILCHARD EGGS TO FOUR SELECTED STAGES OF DEVELOPMENT.

Table 3.-Regression data for figure 1. ($X = \text{temp.}^{\circ} \text{C}$ and $Y = \text{log. time, in hours, in the formula:}$
 $Y = a + b X$)

	Stage III	Stage VI	Stage VIII-IX	Stage XI	Four lines fitted simultaneously
No. items	16	86	46	100	
$\bar{X}$	14.92900	15.00900	14.73700	15.11610	
$\bar{Y}$	1.21278	1.53437	1.72081	1.82242	
a	2.22101	2.39977	2.61754	2.70825	
b	-0.06753	-0.05766	-0.06085	- .05860	-0.05897
Dev.est. ^{1/}	.03720	.03910	.02700	.03180	

^{1/} Standard error of estimate

Table 4.--Time (in hours and minutes after spawning) required to reach a stage of development at different temperatures

Temperature	Stage III	Stage VI	Stage VIII - IX	Stage XI
17.0°C	-	26:17	-	51:31
16.5°C	-	28:05	41:04	55:07
16.0°C	13:49	30:01	44:03	58:58
15.5°C	14:56	32:04	47:14	63:05
15.0°C	16:09	34:16	50:40	67:29
14.5°C	17:27	36:37	54:21	72:12
14.0°C	18:52	39:08	58:18	77:14
13.5°C	20:23	41:50	62:31	82:38

lines in figure 1. First in importance is the time duration of a stage of development which occupies several hours, whereas a sample may be collected during any part of the stage. Consequently, the estimate of age of any given specimen would err, on the average, by a quarter of the time occupied by the stage in the egg's development - a matter of three hours at most. Second, there is the period of time over which spawning is spread (chiefly 8:00 p.m. to midnight), which is represented in our calculations by the midpoint of this time (10:00 p.m.). This might result in an error of as much as two hours in a few instances. Third, not all eggs develop at the same rate even under identical conditions, although the variability resulting from this cause is probably slight. Fourth, there is a possibility of an error in the day of spawning to which a stage is referred; however, an error involving twenty-four hours time should result in a more marked discrepancy than any that have been observed. The temperature data used would also contribute to the variability in so far as it differed from the actual temperature under which the majority of eggs were developing at a station. This could result (1) From the concentration of eggs occurring outside the 10- to 20-meter zone in waters of different temperatures than those occurring in this stratum, and (2) from the temperature data not reflecting the mean temperature for the period of development, as would result if the temperature of the water changed materially during the period from such causes as the stirring action of strong winds^{6/} or upwelling.

However, the variability was not sufficient to destroy either the correlation or the consistency in slope of the regression for the four stages.

Since the Arrhenius equation has been used by previous investigators studying development of fish eggs under constant temperature conditions, it is of some interest to analyze the present data using this formula for the sake of comparison. In doing this the logarithm of rate of development ($\log 1/t$) is plotted against the reciprocal of the absolute temperature ($1/T^{\circ} \text{ abs.}$). When this is done for each record of each of the four stages of development previously analyzed, and a line fitted to the scatter of points for each stage by the method of least squares, as is shown in figure 2, the four fitted lines are, of course, still nearly parallel, and are closely comparable to the lines derived in figure 1.^{7/}

^{6/} The temperature would be lowered if deeper, colder water was mixed with the upper layers through wind action; contrariwise, the temperature could be raised somewhat by a mixing of warmer surface water with the waters of the 10-20 m. stratum by wind action that left depths below this undisturbed.

^{7/} Both methods are included in the paper since, for our purposes, the correlation shown in figure 1 is more usable, while the Arrhenius formulation is needed for comparison of the pilchard with other fishes. The Arrhenius method uses the reciprocals of the values employed in the first method with the exception that the temperature is expressed as absolute temperature.

To compare the effect of temperature on pilchard development with that of development of other fishes, the temperature characteristic (μ), also known as the thermal increment, has been calculated for each of the four stages of eggs and given in table 5. Since the temperature characteristic depends primarily on the slope of the lines, and since the four fitted lines, although nearly parallel, are not exactly so, each stage has a somewhat different μ value. These vary from 25,800 (the value furthest out of line) to 22,100. Since the individual slopes are not significantly different from the common slope (four lines fitted simultaneously) the latter may be taken for computing the average temperature characteristic for the whole period of development, which is 22,500. This is of similar magnitude to the few μ values that have been determined for the development of eggs of other teleosts, which range between 16,700 and 24,900. Hence the pilchard is not atypical, and the observational evidence here used gives substantially the same conclusions as the more commonly used experimental evidence.

SUMMARY

1. The rate of development of pilchard eggs as influenced by the temperature of the water was studied from samples and data collected in nature during the 1940 and 1941 surveys of pilchard spawning off southern California.

2. Evidence based on the time of occurrence of newly-spawned pre-cleavage eggs in the samples indicates that pilchard spawning is largely limited to the four-hour period between 8:00 p.m. and midnight.

3. Experiments conducted on the vessel at sea showed that the pilchard egg ordinarily required about three days to develop to hatching.

4. It is usually possible to separate the eggs according to the several days of spawning represented in the samples, and to determine the probable length of time each stage had been developing.

5. The temperature range over which pilchard eggs were found developing in nature was from 12.5°C. to 17.6°C. However, the majority of pilchard eggs were taken at temperatures between 13.5° C. and 16.0° C.

6. The correlation of temperature with the rate of development of pilchard eggs was analyzed for four stages of eggs. Similar results were obtained for all.

7. There is no evidence that the relation between temperature and rate of development changes during incubation.

8. The time required to reach a stage of development increases about 7.15 percent for each 0.5° C. decrease in temperature.

9. The temperature characteristic (μ) for the pilchard egg during development is about 22,500. This is of similar magnitude to the few μ values determined for the development of other fishes.

FIGURE 2

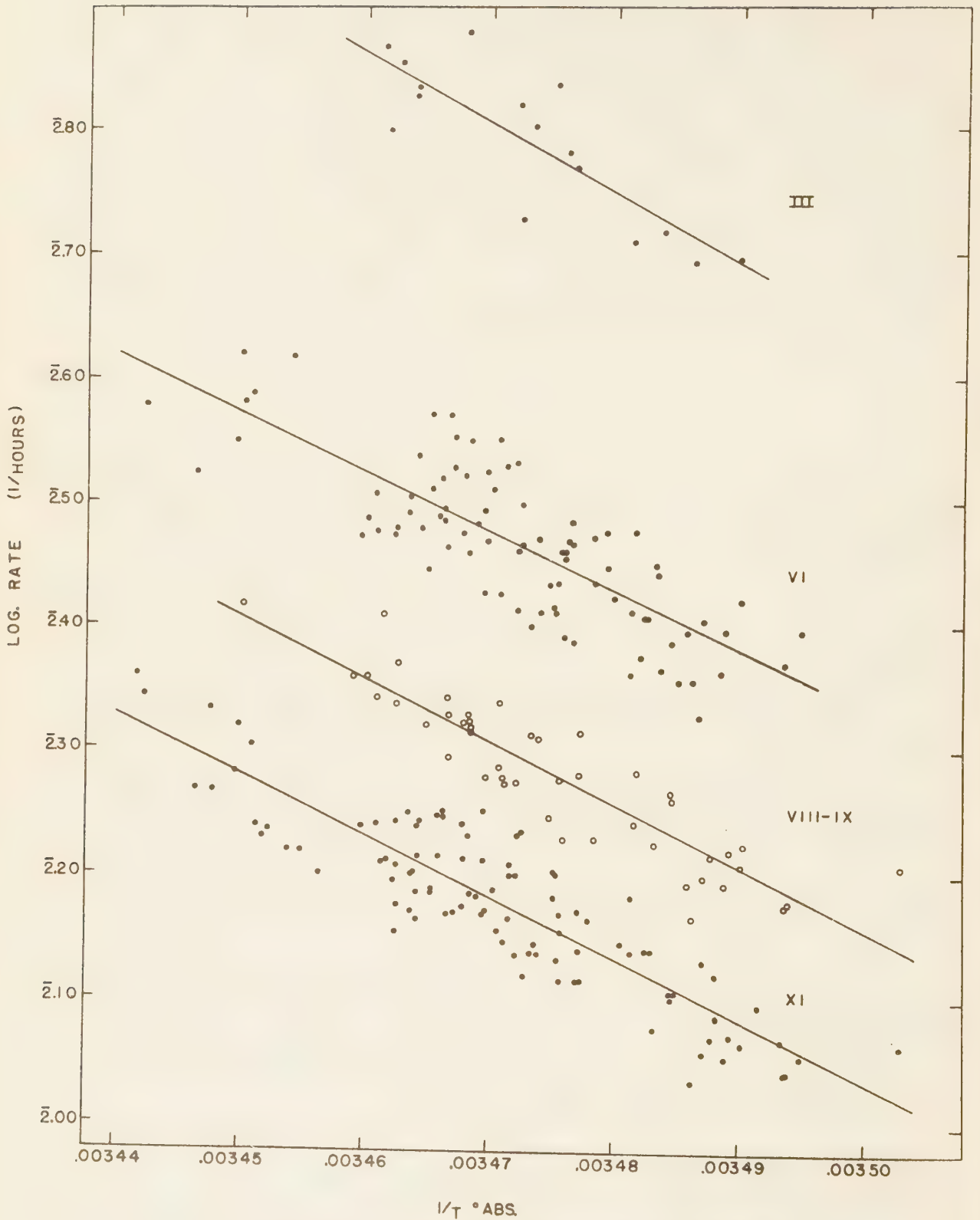


FIGURE 2. - REGRESSION DIAGRAM SHOWING THE INFLUENCE OF TEMPERATURE ($1/T^{\circ} \text{abs.}$) ON THE RATE OF DEVELOPMENT (LOG.1/HOURS) OF PILCHARD EGGS TO FOUR SELECTED STAGES OF DEVELOPMENT.

Table 5.-Regression data for figure 2. ($X = 1/\text{abs. temp.}$ and $Y = 1/\log. \text{ time, in hours, in the formula:}$
 $Y = a + bX$)

	Stage III	Stage VI	Stage VIII-IX	Stage XI	Four lines fitted simultaneously
No items	16	86	46	100	
$\bar{X}$	.00347309	.00347215	.00347544	.00347086	
$\bar{Y}$	8.78722-10	8.46564-10	8.27921-10	8.17758-10	
a	18.25633	15.11103	15.76771	15.12759	
b	-5605.7	-4794.0	-5032.0	-4883.5	
Dev. est. $\frac{1}{\sqrt{}}$	0.0380	0.0390	0.0271	0.0290	
Mu	25,800	22,100	23,000	22,500	22,500

$\frac{1}{\sqrt{}}$ Standard error of estimate.

APPENDIX

The development of the pilchard egg was separated into eleven stages during the investigation of pilchard spawning, a brief description of each of which follows:

Stage I

In stage I were included all pilchard eggs that were not undergoing development, either because they were so recently fertilized that cleavage had not yet begun or because they were unfertilized. Pre-cleavage eggs are usually smaller in size than are pilchard eggs undergoing development; the difference is not in the yolk mass, which is fully as large in the pre-cleavage eggs, but in the width of the perivitelline space, which may be nearly wanting. Many eggs in this stage have an accumulation of protoplasm at the animal pole to form a blastodisc.

Stage II

The period of development of the blastodermal cap is covered in stage II. Although this stage includes the early cleavage divisions, no pilchard eggs have been observed in our samples with fewer than about 128 cells. The lack of material showing early cleavage divisions is hard to explain, especially since stage I eggs were taken previous to initiating cleavage. Such divisions must take place very rapidly, indeed. While the individual cells are fairly large and quite evident, the blastodermal cap has a rugged, berry-like appearance. As the cells become minute and indistinct through repeated divisions, the cap assumes the shape of a smooth, rounded, lenticular dome. The pilchard egg floats with the blastodermal cap downwards. At the opposite end of the yolk mass is the single, large oil globule. This stage persists until segmentation cavity is formed.

Stage III

Stage III covers the period of development from the first appearance of the segmentation cavity to the definite establishment of the embryonic shield. The segmentation cavity is formed when the blastodermal cap separates from the underlying periblast in the middle portion of the cap; the cavity forms somewhat eccentrically, leaving the blastoderm on one side of the cavity somewhat thicker than elsewhere. The thickened area is the region of the developing embryonic shield. However, the outline of the embryo is not definitely defined in this area until after this stage. The germ ring begins the envelopment of the yolk with a cellular sheath; by the end of the stage the ring has enclosed a third of the yolk mass.

Stage IV

This stage begins when the general outline of the embryo can be discerned along the median line of the embryonic shield. The germ ring at the beginning of the stage encloses a third of the yolk mass; the end-point

of the stage is arbitrarily fixed at the period of development when the germ ring encloses four-fifths of the yolk. By the end of the stage the embryo extends about two-fifths of the way around the yolk, with the cephalic region both thicker and wider than the remainder of the embryo.

Stage V

The period of development covered by this stage occupies the final enveloping of the yolk by the germ ring and the closure of the blastopore. The germ ring continues its centripetal growth until the yolk is completely encompassed by a cellular sheath; the final closure occurs just back of the posterior pole of the embryo. While the germ ring is completing this closure, there is a thickening all along the embryo, although the resulting dorsal ridge is still most pronounced in the cephalic region and tapers off posteriorward, so that even by the end of this stage the tail is hardly differentiated from the surrounding tissues, and the embryo itself is a simple, undifferentiated ridge in which somites are not yet defined. Eggs are considered as belonging to this stage until the optic vesicles are distinguishable in the head of the developing embryo.

Stage VI

This stage begins after the closure of the blastopore when the outline of the optic vesicles can be seen in the cephalic region of the embryo; it ends when the tail starts to separate from the yolk. The optic vesicles occupy fully half of the head during this stage; the somites take shape, being evident all along the embryo except in the immediate vicinity of the head and tail; the embryo extends about two thirds of the way around the yolk; the single oil globule in the yolk is a little beyond the posterior end of the embryo and retains this position in the yolk mass subsequently. This stage is of longer duration than any of the preceding three. By the end of the stage, the pupils can be discerned in the eyes, the embryo is about of equal thickness along its entire length, while the tail is somewhat swollen at its tip.

Stage VII

This stage commences when the tail begins to separate from the yolk mass; it covers the early growth of the tail until the free portion is about of equal length to the head of the embryo. Although the demarcation of the beginning of this stage is rather definite, its termination is somewhat arbitrary. All the remaining stages are separated primarily on the degree of development of the tail, as it offers the best landmarks on which to base separation into stages. During Stage VII the tail remains of uniform thickness along its length; the posterior end is rounded and even appears somewhat swollen in some individuals; the fin fold is barely discernible, extending around the free portion of the tail and along the dorsal side of the body to near the region of the head; there is either no differentiation of somites in the free portion of the tail or at best a few somites are formed at the base of the tail by the end of the stage; along the rest of the body the somites stand out sharply when viewed from above. By the end of this stage in most specimens the free tail extends up to, but not beyond, the position of the oil globule.

Stage VIII

At the beginning of this stage the developing tail is free from the yolk mass for a length greater than the length of the head; by the end of the stage about one-third of the body at the tail end is separated from the yolk. The fin-fold is becoming conspicuous, although it is barely half as wide as the embryo by the end of the stage. The intestine can be seen as a line along the ventral side of the developing tail, and the position of the vent is indicated in the fin-fold. Somites are formed along the tail, at least as far as the end of the intestine. The tail tapers posteriorly, but the tip is still rounded.

Stage IX

Approximately one-third of the body is free from the yolk at the beginning of the stage and the tail is often bent to one side; by the end of the stage the tail is always curved, either to the right or left of the yolk, and comprises about two-fifths of the total length of the embryo. The fin-fold is about half as wide as the body at the beginning of this stage, it is somewhat broader along the free ventral portion of the body than along the dorsal side; by the end of the stage the ventral fin-fold is nearly as wide as the body proper. During stage IX pigment spots (melanophores) may appear on the dorsum in two parallel rows, one on either side of the notochord, with the spots more numerous immediately behind the head; on some specimens pigmentation does not appear until after this stage. The embryo conforms less to the shape of the yolk than previously and is beginning to straighten in its middle portion; at the end of this stage the tail is curved to one side of the yolk at about a 45° angle to the plane of the embryo.

Stage X

The free tail comprises at least two fifths of the length of the body at the beginning of the stage and is as long as the remainder of the body by the end of the stage. During stage X a fundamental change in the orientation of the embryo is completed, a change begun in the previous stage. This is accomplished by the straightening of the body of the embryo and the upward flexing of the tail. The embryo as a whole is no longer curved around the yolk; rather the plane of orientation has been rotated a complete 90° . Only the head end remains curved around the yolk, the remainder of the body being straightened out into one plane, although it is U-shaped due to the flexing of the end of the tail. During this stage the tail increases in length, until its tip is nearly as far forward as the base of the head; the fin-fold is about as wide as the body along the dorsal side and somewhat wider along the ventral margin.

Stage XI

This is the last stage before hatching. At the beginning of the stage the tail stretches as far forward as the base of the head, and the posterior portion of the body free from the yolk sac is longer than the portion carrying the yolk sac, and this disparity increases during the stage.

The yolk mass is now oval-shaped; the fin-fold is wide, being 1 1/2 to 2 times as wide as the body; the tail is divided into somites to its very tip, which is now somewhat pointed. The eyes are still colorless, pigmentation taking place after hatching. This stage ends with the hatching of the egg.

KEY to Plates

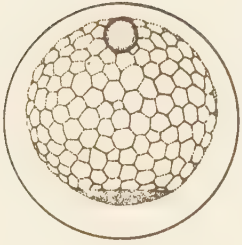
Plate 1

- Fig. 1 - Stage I
- " 2 - Stage II, fairly early
- " 3 - Stage II, late
- " 4 - Stage III, intermediate, dorsal view
- " 5 - Stage IV, beginning
- " 6 - Stage V, beginning
- " 7 - Stage V, immediately before closing of
blastopore, ventral view
- " 8 - Stage VI, early
- " 9 - Stage VI, late

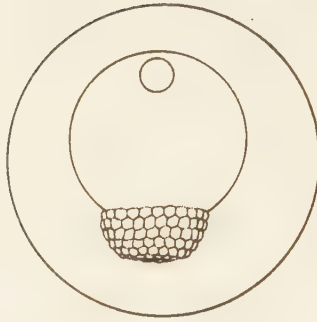
Plate 2

- Fig. 10 - Stage VII, early
- " 11 - Stage VII, late
- " 12 - Stage VIII, late
- " 13 - Stage IX, late
- " 14 - Stage X, early, dorsal view
- " 15 - Stage X, early
- " 16 - Stage XI, early
- " 17 - Stage XI, intermediate, dorsal view
- " 18 - Stage XI, late

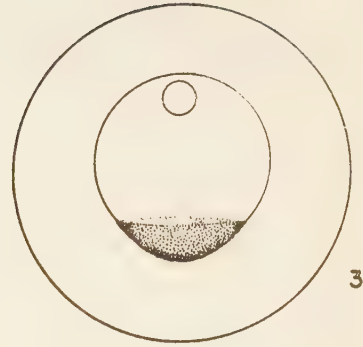
PLATE I



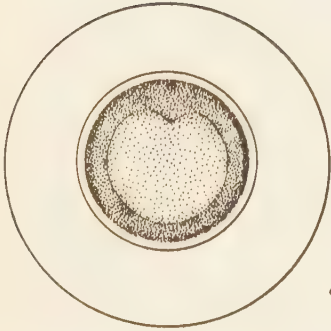
1



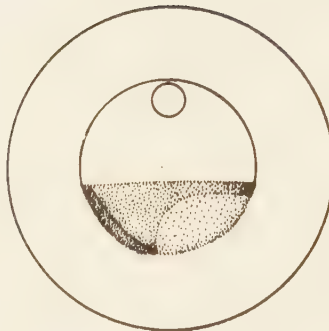
2



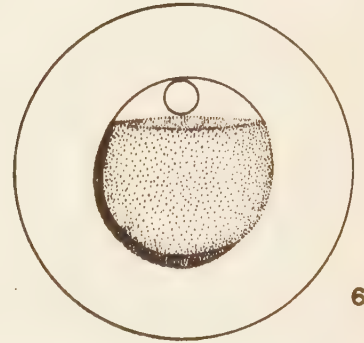
3



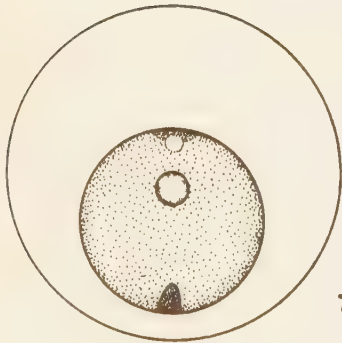
4



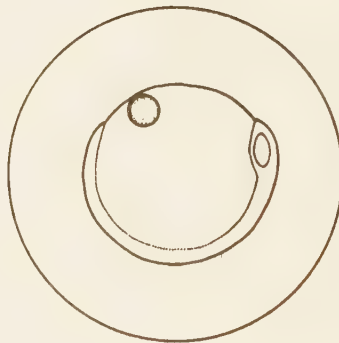
5



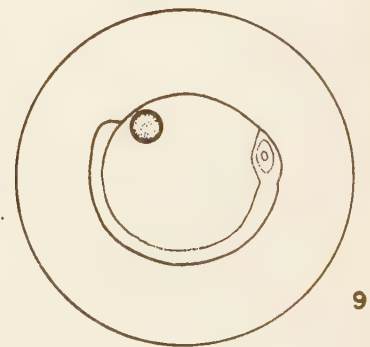
6



7



8



9

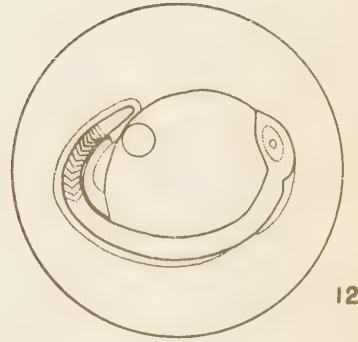
PLATE 2



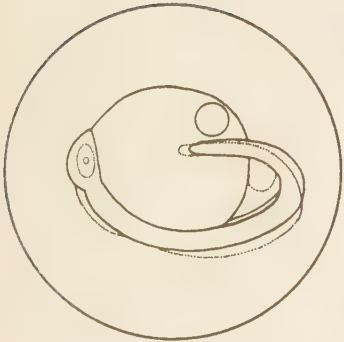
10



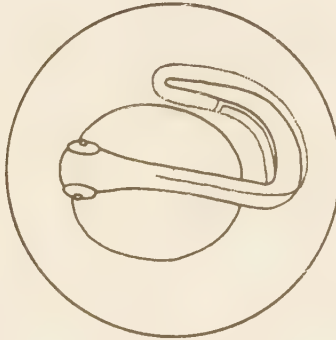
11



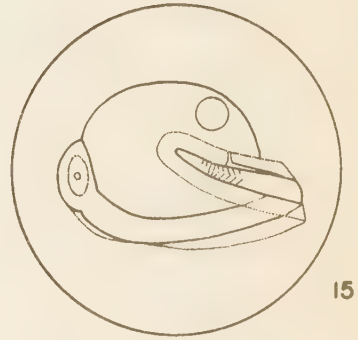
12



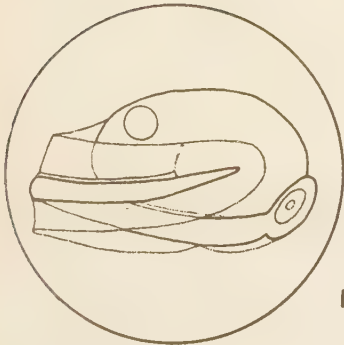
13



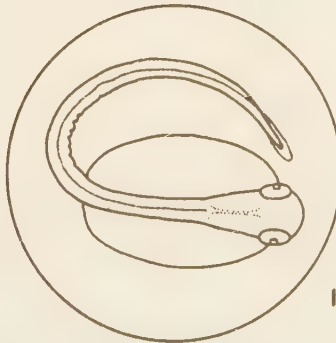
14



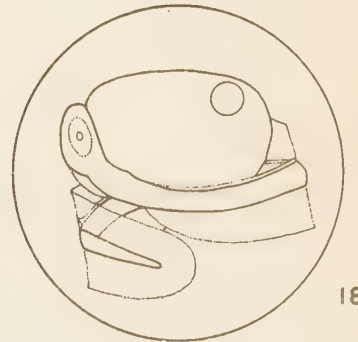
15



16



17



18

Table 6.-Stages of pilchard eggs in sorted portions of spawning survey samples

Station	Time	Temp.	STAGE OF DEVELOPMENT											
			I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
101	4:20	13.95		1		1			10	12			*4	
102	9:45	14.40		9				*4			4	7		
103	14:10	13.62		2				*15			*15		*11	
104	18:30	13.92				24		56	20	1	2	226	202	
105	22:45	14.24	6			11	56	1	140	1			*28	
108	6:15	13.40							2	4			*2	
109	2:30	14.59					2				*22		*17	
110	18:00	15.63					6			*300			1	
111	1:55	13.68					7						*11	
112	22:30	14.10	15			25	32	7	243		1	28	*385	
113	18:30	13.98			3	546		59	54	1	3	92	38	
114	11:15	15.35	2	7	*1072	13	1	19	40				*6	
115	7:30	15.36		6				*19				4	*18	
117	13:00	15.89				5			1	*15		2		
118	15:00	14.62		7	*74	2		*170	28			5	8	
119	11:00	15.66			10			5	7				*4	
120	20:55	15.32												
121	16:40	15.79				1	5		1	*12	*14		*6	
122	8:20	14.97		58		3		*57	2		1		*5	
123	19:50	15.46			4	40				*2				
124	15:40	14.75	1					2	20				*24	
125	11:30	15.11						*10	1			8	1	
126	6:30	15.52						*7				2	*16	
127	2:00	15.42						*6				12		
128	6:00	15.48	1					*3			14			
129	1:40	15.33						2					*7	
130	23:55	14.25					1	2				2		
131	7:40	16.04		21		3	16	2	3			3	3	
132	11:35	15.90	1		*36			*53	67			1	*28	
133	18:20	15.47											*13	
134	18:15	15.44				25	48	7	52	1	3	15	40	
135	12:00	15.79			*17				16				*3	

*Stages marked by an asterisk were used in the correlations discussed in the body of the paper. Separation into days is indicated as follows: Stages that have been developing one to two days or three to

Table 6. Continued

Station Time pre- Temp.
served

Stage of Development										
I	II	III	IV	V	VI	VII	VIII	IX	X	XI
136				5			*8	*1		
137										
138	82	2		1	*22			*72	1	3
139	1	*45			*78			2	16	
140			6			70				40 *15
201				3	*257					
202	7				*34	58		31	75	117
203	2	*90	6	1	*56		*13	*2	52	16
204				19			1	3	15	
205					*2		*8			*7
206					1			9		
208				3		2		1	1	
209								1		1
210						3				
211	1			1	2				6	3
212	4				*4	7			2	4
217		26	10	1	*215	2			12	
219			1	13			1	24		
220				2			*18	*13		
221	9				*3		*5	*3		*2
222	74				*58				7	1
223			21	15		13			33	
224	1				*110			10	22	2
225					3	1			1	*6
228										
229	1		1			2				1
230		*4			8	6				
					*145	1			61	36

*(Cont'd.)

four days are underlined, while stages spawned within twenty-four hours of collection or two to three days prior to collection are not underlined. When only one group of stages is underlined at a station, the age is between one to two days, except at stations 108, 323, and 612 (three to four days). A spawning day commences at 22:00 o'clock.

Table 6. - Continued
Stage of Development

Station Time pre- Temp.
serv.d

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
231	22:20	14.74			4		3				
232	4:45	15.31				*11			20	1051	135
234	10:50	14.73			1	1			11	22	
235	0:50	15.66				*29		1	11	4	
236	5:40	14.96				*33				1	
237	11:30	15.22				14					*80
238	15:35	15.26	1	157			9				*29
239	20:00	15.12		2	98		6	*31			*28
240	1:00	15.82			87				1	57	3
301	4:15	13.71									2
302	18:10	13.54	*5				1		3		
303	23:35	12.95									
304	4:40	13.26									
305	9:40	13.50									1
306	13:45	14.90	*13	1	38	5		*4			
307	17:55	14.64		20	2	*3				7	2
308	14:10	13.87			3	1	49			48	30
309	15:05	13.98	9			*15		*3	*8	2	4
310	6:30	14.60	2		19	*4		1	6	2	
311	9:50	14.43			19	20			9	5	1
314	9:05	14.48			19	39	29	41	43	15	3
315	4:40	14.76				1			*9		
316	23:00	15.49				1			1	2	
317	23:10	15.00			4	5	37	18			*3
319	23:55	14.66			1				1		
320	9:55	15.60				2					
321	4:45	15.16				*187	1			3	4
323	13:25	13.25					22	16	6	16	5
326	21:55	15.60							4	3	*19
327	16:15	15.74			1				*9		
328	18:55	15.46		11			2	1			1
329	13:40	15.82		48			6	15	1		
330	13:15	14.14	2		2	*115	1				*3
			10						43	78	1

Table 6. - Continued
Stage of Development

Station Time pre- Temp.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
331	19:25	14.38	1	1		6	7		15	114	45
332	3:35	15.42				*4	1			31	
333	9:20	15.46	2			1				2	3
334	15:15	14.38	1							14	2
335	23:15	15.49			1						
336	4:15	15.50				*48		1		23	9
337	9:50	14.58									
338	17:00	14.78				1					1
340	7:10	15.80				*5					*5
401	3:00	15.68									1
402	17:20	14.18	5	2		13	26	21	2	11	7
403	23:40	12.68									1
404	5:00	13.97					4	*25			*9
405	10:40	13.59			9			*35			*14
406	14:15	13.12			18				1		*2
407	18:15	13.84	*5			*2			*2		*6
408	13:15	13.80				*11	11			2	2
409	13:25	13.76	1			31			*58	1	*9
410	18:35	16.26				*146					
411	8:40	14.70							19	8	1
412	22:30	13.84				*36				2	2
413	17:30	14.24		31		8	2		18	476	87
414	8:40	14.69	871	23	14	*540	16	2	142	93	30
415	4:25	13.98		1	262	*281		37	*4		*28
416	23:10	14.85		2	359		43	*208	2	1	*25
417	13:30	15.49						*305			
418	18:10	13.93	3	7		*26				10	3
419	12:40	15.52			1						
420	22:00	16.02									
421	17:20	15.84									
422	7:45	13.68	10				2	1	*4		*8
423	2:45	15.20			4			*1			2
424	22:30	14.57			8		4	*63		4	*16
425	12:35	14.99	1			*8					1

Table 6. - Continued

Station Time pre- Temp.

served		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
426	7:10											
427	12:40											
428	7:30											
429	2:40											
430	13:10											
431	19:30		1									
432	1:15											
433	7:25											
434	8:10											
435	23:30											
436	4:00											
437	9:00											
438	13:35											
439	17:45											
440	0:00											
501	5:05											
502	20:20											
503	2:20											
504	7:25											
505	12:10											
506	16:40											
507	21:10											
508	15:25											
509	15:40											
510	12:15											
511	11:00											
512	2:45											
513	20:10											
514	12:00											
515	7:45											
516	2:30											
517	4:35											
518	7:25											
519	5:30											
520	14:50											

Table 6. - Continued

[illegible]

Table 6. - Continued

[illegible]

Table 6. - Continued

Station	Time pre- served	Stage of Development										
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1721	14:35			*3				15	1			1
1722	10:15		59	1			25	230			1	*10
1723	6:05		11				*58				9	*86
1724	1:55						102	4	14	122	195	58
1725	21:40				1	713			*6	*12		1
1726	17:30	1			12	28		4				*2
1727	13:10			*5		1	7	3		1		*6
1728	8:40		41			1	*332				39	*176
1730	17:50					1			161	412	152	
1731	22:05	79	1			56	457			1	32	43
1732	3:00		1			2	2	1				
1733	10:20		38	50			12	53		1		*4
1734	6:15		28				*58	2			3	*46
1735	1:45		9			8	*122	4	*89	*79	1	
1736	21:25				35	842		667	76			*11
1737	17:45				44			1136			1	*103
1740	17:40					1	4					*4
1741	16:05				1	436						
1742	12:20	1	1	16	28	1		7	2	69	193	
1743	8:00	4	633	1		1	42	146	*53	*19		
1744	20:25	18			1	43	150		1			*14
1745	1:15		1		1	1038	3062			3	31	84
1746	7:10		38				*22			7	77	81
1747	11:20		2	4			20	279				*27
1751	22:00	1				1	*33					*135
1752	20:45	4			1	10	30	1	1	4	5	*20
1753	2:10		21				*175					*75
1754	7:35		420				*252	1			5	*306
1755	12:55		1	10	90		3	26			5	15
1760	17:35					8			12			*14
1761	4:00		38		1		*97	13			1	*57
1762	8:50		56	14			9	41			1	*5
1763	13:45			3	4	1		12	11			
1764	20:00			1		26		1	2	15	7	

Table 6. - Continued

Table 8. - Continued

Station

Time pre-
served

Temp.

I

II

III

IV

V

VI

VII

VIII

IX

X

XI

XII

Stage of Development												
I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
1911	7:30	14.08										
1912	11:15	13.83										
1913	15:55	13.90										
1914	21:40	14.19										
1915	2:55	14.71	9	15	1	3						
1916	8:00	14.65		14	14							
1917	12:50	14.74		1	*9							
1920	12:50	14.84	1		*32							
1921	21:50	15.64			2							
1922	17:50	15.23										
1923	14:05	14.48			2							
1924	9:35	14.08	5	5	105	87						
1925	7:25	14.41	3	13	145	24						
1926	2:35	14.70	71	38	*270	86						
1927	21:30	14.87	9	32	18	29						
1928	16:45	15.35	1	18		55						
1930	1:05	13.80	1			15						
1931	11:35	16.47										
1932	20:40	15.70										
1933	3:00	15.66										
1934	8:05	15.20	1		*2							
1935	12:45	14.24	31	1	*47							
1936	18:30	14.52			*127	1						
1937	00:55	15.45	149		40	380						
1940	6:25	15.24	1	5	*25	1						
1941	9:25	16.61										
1942	6:10	16.60										
1943	22:25	16.49	1		1							
1944	18:25	15.66										
1945	14:45	15.00										
1946	10:40	14.48	1		*1953	1						
1947	7:55	14.86			*46	18						
1951	00:10	16.84			*2	3						
1952	23:45	16.78	1		*58	1						
1953	19:25	16.80			3							

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18

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*28

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*39

71

9

48

*140

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Table 6. - Continued

Station	Time pre- served	Stage of Development										
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1954	14:15		2					6				
1955	8:45	1	97				*72	1		1	15	*118
1960	19:20											
1961	5:20											
1962	10:35							1				2
1963	15:05		1					2				*2
1964	20:10				1	3		10	*55	*1		*2
2111	2:30											
2112	7:50											
2113	12:35	7	186	70		2	271	1				1
2114	17:45				89	164	2	535		9	31	51
2115	23:45	4				4	3	201	4		1	*46
2116	5:15		4				*149	104	73	2		*41
2117	10:00										37	77
2120	12:55								1			
2121	21:30					1						
2122	17:30				1				1			
2123	14:15				1							
2124	7:35		303			1	34	10				*26
2125	4:05		2									1
2126	20:25											
2127	19:10											
2128	15:00											
2130	00:45		1				*10	2				
2131	5:35											
2132	9:55		2					2				
2133	13:55			1								
2134	17:25				2							
2135	21:30	5			20	40	48	93	44	4	15	*109
2136	2:05					11	48	296	5	5	16	*199
2137	6:35						8	121	44	5	8	*253
2140	00:15		10				*3		1			

Table 6. - Continued
Stage of Development

[illegible]

used Stage of Development

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Cruise dates of collections listed in Table 6

<u>Cruise No.</u>	<u>Station No.</u>	<u>Date</u>
1	101-140	March 5-14, 1940
2	201-240	March 20-28, 1940
3	301-340	April 4-14, 1940
4	401-440	April 22-May 3, 1940
5	501-542	May 10-19, 1940
6	601-642	May 27-June 7, 1940
17	1711-1764	March 21-30, 1941
19	1911-1964	April 14-25, 1941
21	2111-2164	May 8-17, 1941
23	2311-2364	June 2-12, 1941
25	2514-2535	June 27-30, 1941

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5. A Method of Computing Mortalities and Replacements

By

Ralph P. Silliman 1/

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INTRODUCTION

The place of estimates of mortality and replacement in a management program, and their position in the investigation of the pilchard resource of the Pacific coast, are pointed out by Sette (1943). Derivation of such statistics for fish populations has been investigated by Baranov (1918), Thompson and Bell (1934), and Ricker (1940), whose theories underlie the computations described herein. The last named student has developed concepts not included in the work of the earlier authors and gives mathematical formulations in a form more readily adaptable to the data available for the pilchard population than do the others. This report describes the application of Ricker's formulations to the pilchard data, and also develops new equations where necessary. To avoid adding to the symbols in the already confused set employed in fisheries statistics, those used by Ricker are adapted for this report.

This analysis was conceived and carried out under the inspiration and guidance of Oscar Elton Sette, in charge, South Pacific Investigations of the United States Fish and Wildlife Service. For critical reading of the manuscript and suggestions for improvement, the author is grateful to Drs. W. E. Ricker, M. B. Schaefer, J. L. Hart, and Frances N. Clark.

BASIC ASSUMPTIONS

In treating fisheries statistics by the method used herein it is necessary to make certain simplifying assumptions. These have been set forth by Ricker (p. 44) and may be condensed as follows:

1. The amount of effort expended toward catching fish is distributed uniformly over the geographical range of the species during the fishing season.
2. There is no competition between units of fishing gear for fish to be caught during one and the same instant.

Of the two types of fisheries postulated by Ricker, his "Type II" most nearly conforms to that of the pilchard fishery. It differs from his "Type I" in that natural mortality and recruitment take place during the fishing season. The listed assumptions are given by Ricker as applying to his "Type I" fishery, but are later implied to be inherent in "Type II" also (Ricker, 1940, p. 59).

They do not hold strictly true for the pilchard fishery, especially with regard to the uniform distribution of fishing effort. This does not preclude the use of the involved formulations, however, if it is kept in mind that they apply only to the extent to which the basic assumptions hold true.

KNOWN QUANTITIES AND RELATIONSHIPS

Use of the series of formulations given in this report is based on the assumption that the fishery has been stabilized at two different levels of exploitation during its development. Although the pilchard fishery has never reached complete stability, there were two periods during its history within which there was little shift in the total catch, and apparently little trend in the total fishing effort expended. The first period occurred when the expansion of the industry was temporarily halted by the economic depression of the early thirties and the second included the recent years of the fishery, during which the total catch, after having reached a maximum in the 1936-37 season, has fluctuated around an annual take of about half a million tons per year.

Uniform recruitment, as well as uniform exploitation, are requisites of a stabilized fishery. During the early years of the pilchard fishery, most of the recruitment was furnished by unusually successful age groups or broods, which occurred at intervals of about four years. Four "super-abundant groups" have been recognized by Clark (1936) during the 15 seasons, 1919-20 to 1932-33. To average out these fluctuations in recruitment, the first period used in the study was chosen to include the passage through the fishery of two of the successful broods (designated groups "C" and "D" by Clark, 1936) and included the fishing seasons 1925-26 through 1932-33, thus representing a time somewhat prior to the depression. During the more recent period (1937-38 through 1941-42) the dominance of unusually successful groups has largely disappeared, (Clark, 1939 p. 21) indicating more uniform recruitment.

For each of the two levels of exploitation under consideration, it is necessary to have information on: (1) Age composition of the stock available to the commercial fishery, (2) total catch per season, and (3) relative amounts of effort (product of gear and time) expended per season. For the more recent of the two periods, age composition was determined from scales. During the earlier period scale readings were not taken and it was necessary to deduce age composition from length composition by a method involving growth rate and other characteristics of year classes. The total catch records were obtained from the weigh-in reports of the industry and converted to numbers by means of length distributions in samples of the catch in conjunction with previously determined length-weight relationships. Relative amounts of effort were calculated by dividing the total catch by the computed catch-per-unit-of-effort.^{1/}

Numerical values obtained for the three items of information are given in the accompanying Table 1. The data on age composition are from samples taken in the commercial fishery throughout each fishing season, exclusive of the summer fishery carried on in the Pacific Northwest.

^{1/} This computation is in process of revision (1943).

Samples for the eight seasons of the early period were combined to discount the effect of fluctuating recruitment. For the latter period, when recruitment was more uniform, age readings for the last season (1941-42) only were used.^{2/}

Table 1.-- Numerical values determined for age composition, relative fishery effort, and catch.

Period	: Hundreds of fish in samples of age (to last birthday):													: Rela-	: Catch,
	: 1:	: 2:	: 3:	: 4:	: 5:	: 6:	: 7:	: 8:	: 9:	: 10:	: 11:	: 12:	: 13:	: effort	: billions of fish
1925-33	:47:	:186:	:558:	:338:	:202:	:120:	:72:	:43:	:25:	:13:	:10:	:5:	:3:	:1:	:1.66
1937-42	:58:	:527:	:310:	:56:	:14:	:2:	:1:	:	:	:	:	:	:	:4:	:4.98

The numerical values given in Table 1 represent the results of a canvass of the data available at present. Many shortcuts and approximations have entered into their derivation, but they have been used in the computations to obtain a preliminary estimate of the changes which have taken place in the pilchard stock, and to show the way in which more precise data may be used when available. The analyses necessary to the derivation of such precise data are now being carried on by the United States Fish and Wildlife Service and the California State Fisheries Laboratory.

DETERMINING TOTAL MORTALITY

The rate of disappearance, or total mortality, of the year classes may be determined from the relative age composition of the stock. As pointed out by Baranov (1918), in a stabilized population, the numbers of fish of each age, starting with the youngest commercial-size, are the same as the numbers of a given year-class surviving each year since its entry into the fishery. Therefore, the effective rate of disappearance may be determined from the age composition of the stock at any time after stabilization at that rate. The simplest method is to plot the logarithms of the numbers of fish of each age, so that a constant percentage decrease

^{2/} A recent study of the method of taking scale samples for use in the age analysis indicated that there was a tendency to select the larger fish of each sample (scales were taken from only 10 fish out of each 50 measured) for the removal of scales. This may have caused an indicated mortality rate lower than the actual. Computations to correct for this selection are now being made.

will be represented by a straight line. Figure 1 shows in this fashion the numerical values used in this paper. It will be seen at once that in both periods the numbers of fish over age two decline at a constant rate^{3/}, while those of ages one and two years do not. It was assumed that the one- and two-year-olds are not fully available to the fishery, and the line was fitted to the other ages by inspection. The lines shown indicate an annual decline in logarithm of .225 for the first period and .700 for the second. These may be translated into mortality rates (a) by the following formulations:

Let S_1 and S_2 be the relative stocks of any two successive ages.

$$\text{Then } S_2 = S_1 - aS_1 = S_1(1-a)$$

$$\text{and } 1 - a = \frac{S_2}{S_1}$$

$$\text{taking logs} \quad \log(1-a) = \log S_2 - \log S_1$$

$$\text{or} \quad \log(1-a) = -(\log S_2 - \log S_1) = -(\text{annual decline in log})$$

Substituting numerical values given above, and letting subscripts refer to the two periods, we have:

$$\begin{array}{lll} \log(1-a_1) = -.225 & 1-a_1 = .60 & a_1 = 1-.60 = .40 \\ \log(1-a_2) = -.700 & 1-a_2 = .20 & a_2 = 1-.20 = .80 \end{array}$$

In other words, the total mortality, or rate of disappearance, as indicated by the age compositions of the stocks, was 40 percent for the first, and 80 percent for the second, period.

SEPARATING FISHING MORTALITY FROM NATURAL MORTALITY

The total mortalities determined above may be broken down into fishing mortality and natural mortality if the latter is assumed to be the same for the two periods. In the absence of any evidence of a change in the rate of natural mortality, this assumption was made, and the method noted below was adopted.

This depends upon the fact that, with the same natural mortality (n) for two periods, a given pair of total mortalities (a_1, a_2) combined with a given ratio between the two fishing mortalities (m_1, m_2) is associated with a certain ratio between the amounts of effort (F_1, F_2) expended per year during the two periods. The procedure is to determine what ratio ($R = \frac{m_2}{m_1}$) between the two fishing mortalities gives the known ratio between

^{3/}The regular decrease in numbers of the fish in each age class for the earlier period is a result of the method of age analysis employed, rather than a natural phenomenon.

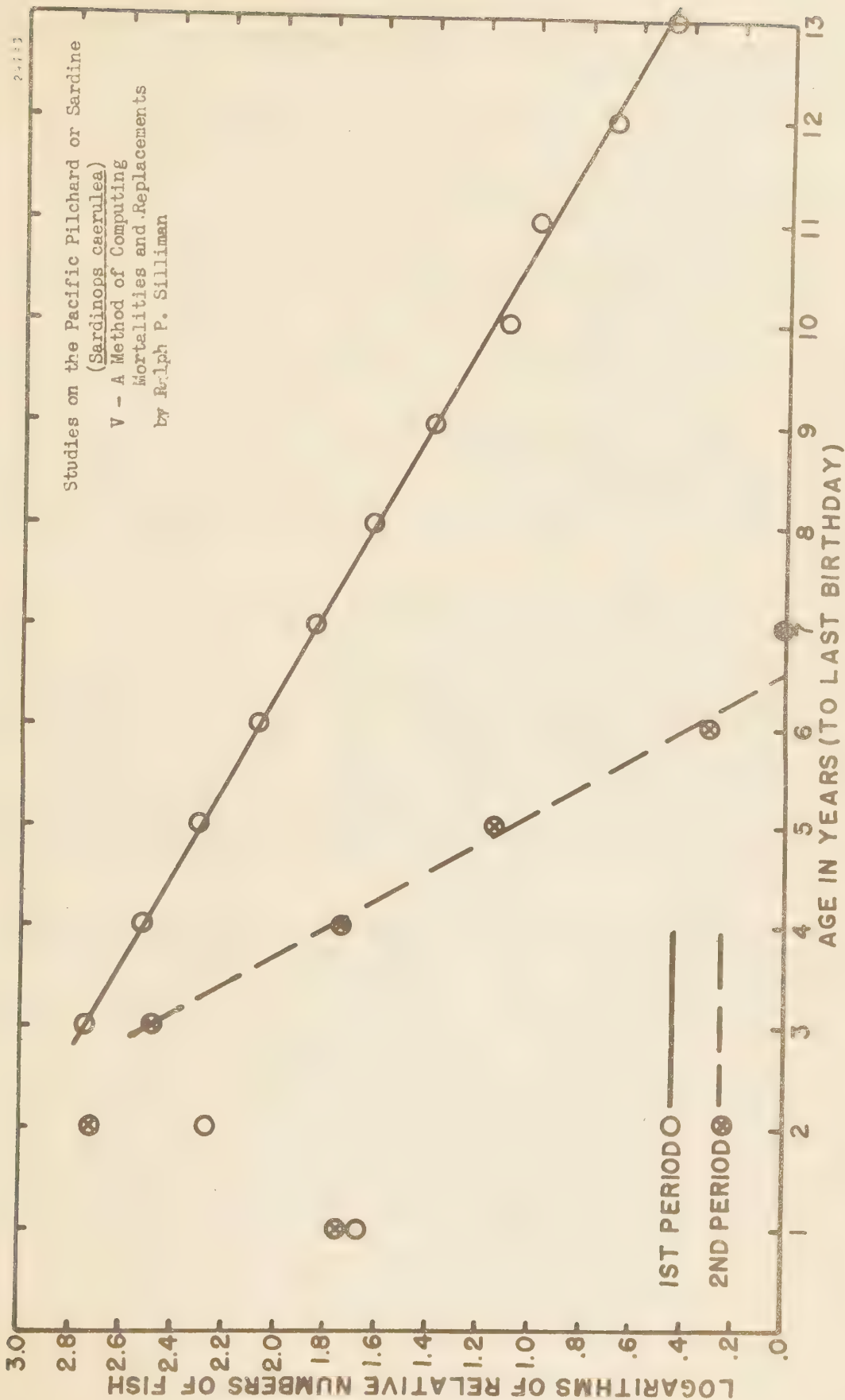


Figure 1. Relative age compositions of the stocks in the two periods of the pilchard fishery mentioned in the text.

the two amounts of effort ($\frac{f_2}{f_1} = 4$). Natural mortality (n) is put in terms of R , a_1 and a_2 as follows:

$$a_1 = m_1 + n - m_1 n \quad (\text{Ricker, p. 60, 1st paragraph})$$

$$a_2 = m_2 + n - m_2 n$$

$$\text{But, by definition: } R = \frac{m_2}{m_1} \text{ and } m_2 = Rm_1$$

Substituting in the second equation above we have: $a_2 = Rm_1 + n - Rm_1 n$

Multiplying the first equation by R : $Ra_1 = Rm_1 + Rn - Rm_1 n$

Subtracting from the last equation the one above it:

$$Ra_1 - a_2 = Rn - n = n(R - 1)$$

$$\text{and } n = \frac{Ra_1 - a_2}{R - 1} \quad (\text{I})$$

Now $\frac{f_2}{f_1}$ must be gotten in terms of R , n , a_1 and a_2 as follows:

$$\text{Starting again with: } a_1 = m_1 + n - m_1 n$$

$$\text{and transposing: } a_1 - n = m_1 - m_1 n = m_1 (1 - n)$$

$$\text{Dividing by } (1 - n): m_1 = \frac{a_1 - n}{1 - n} \quad (\text{II})$$

$$\text{Also, by definition: } m_2 = Rm_1 \quad (\text{III})$$

$$\text{Finally: } \frac{f_2}{f_1} = \frac{\log (1 - m_2)}{\log (1 - m_1)} \quad (\text{IV})$$

This last formula was developed by Ricker for fisheries of Type I. However, as shown by Schaefer (1943), it may be used equally well for fisheries of Type II.

Starting with a value of R of 2.4 and substituting our previously determined values of a_1 (.40) and a_2 (.80), $\frac{f_2}{f_1}$ may be computed from the above equations as follows:

$$(I) \quad n = \frac{2.4(.40) - .80}{2.4 - 1} = .11143$$

$$(II) \quad m_1 = \frac{.40 - .11143}{1 - .11143} = .3226$$

$$(III) \quad m_2 = 2.4(.3226) = .7742$$

$$(IV) \quad \frac{f_2}{f_1} = \frac{\log (1 - .7742)}{\log (1 - .3226)} = 3.82$$

Table 2.--Substituting successive values of R at intervals of .1, we have the following:

R	n	m_1	m_2	$\frac{f_2}{f_1}$
2.4	.1143	.3226	.7742	3.82
2.5	.1333	.3077	.7692	3.99
2.6	.1500	.2941	.7647	4.15

Obviously, the value of R most closely approaching the true value is 2.5, since the value of $\frac{f_2}{f_1}$ of 3.99 is closest to the empirical value of 4.0. Considering the variability of our data, any interpolation of values of R would be superfluous. Therefore, referring to the center line of the table, we now have natural mortality and fishing mortality for the two periods.

DETERMINING RATE OF RECRUITMENT

To obtain the number of recruits entering the fishery each year, we must first obtain the size of the available stocks for the two periods. These may be computed from the total catch statistics, if it is known what fraction the catch is of the available stock in each period. Ricker calls this fraction, "rate of exploitation" (μ). Its value may be determined from our previously computed values of total mortality (a), fishing mortality (m), and natural mortality (n) as follows:

$$\mu = \frac{m}{m+n} (m+n-mn) \quad (\text{Ricker, p.60, par. 2})$$

$$\text{But also: } a = m + n - mn \quad (\text{Ricker, p.60, par. 1})$$

$$\text{Substituting: } \mu = \frac{am}{m+n} \quad (\text{V})$$

Using the numerical values of a, m, and n given above, we have:

$$(\text{V}) \mu_1 = \frac{.40(.3077)}{.3077 + .1333} = .2791$$

$$(\text{V}) \mu_2 = \frac{.80(.7692)}{.7692 + .1333} = .6819$$

Since μ represents the fraction of the stock caught by the fishery, the available stock (S_A) may be computed from the catch (c) and rate of exploitation (μ) by the simple relationships:

$$c = \mu S_A \quad \text{or} \quad S_A = \frac{c}{\mu} \quad (\text{VI})$$

Substituting the values of μ and c previously determined:

$$(VI) \quad S_{A1} = \frac{1.66}{.279} = 5.95 \text{ billions}$$

$$(VI) \quad S_{A2} = \frac{4.98}{.682} = 7.30 \text{ billions}$$

These stocks may now be broken down into their component ages in accordance with the previously determined relative age compositions.

Table 3.--Numbers of fish of each age obtained

: Billions of Fish of Age (to last birthday):													
Period:	1	2	3	4	5	6	7	8	9	10	11	12	13
1	.18	.68	2.04	1.23	.74	.44	.26	.16	.09	.05	.04	.02	.02
2	.44	3.98	2.34	.43	.10	.02							

Since the fish of age one are not fully available to the fishery, it is necessary, in order that the recruitment to age one may be determined, to work backward from the first age class that is fully available, age three in our example. Let s_1 and s_2 be the available stocks of any two successive age classes, and S_1 and S_2 be the total stocks of these two age classes, respectively. If the stock of the second age class is considered fully available, $s_2 = S_2$. s_1 is subject to the full mortality rate a , but the balance of the age class ($S_1 - s_1$) is subject only to natural mortality n . Formulating these statements we have:

$$s_2 = S_2 = S_1 - as_1 - n(S_1 - s_1)$$

$$\text{Expanding:} \quad s_2 = S_1 - as_1 - nS_1 + ns_1$$

$$\text{Transposing:} \quad s_2 + as_1 - ns_1 = S_1 - nS_1$$

$$\text{Factoring:} \quad s_2 + s_1(a - n) = S_1(1 - n)$$

$$\text{Dividing by } (1 - n): \quad S_1 = \frac{s_2 + s_1(a - n)}{1 - n} \quad (VII)$$

Substituting the empirical values previously determined and letting subscripts refer to ages, we find for the first period:

$$(VII) \quad S_2 = \frac{2.04 + .68(.40 - .13)}{1 - .13} = 2.55 \text{ billions}$$

$$(VII) \quad S_1 = \frac{2.55 + .18(.40 - .13)}{1 - .13} = 2.99 \text{ billions}$$

And similarly for the second period:

$$(VII) \quad S_2 = \frac{2.34 + 3.98(.80 - .13)}{1 - .13} = 5.76 \text{ billions}$$

$$(VII) \quad S_1 = \frac{5.76 + .44(.80 - .13)}{1 - .13} = 6.95 \text{ billions}$$

In other words, the estimated annual recruitment to age one during the second period was about two and a third times what it was in the first period.

EFFECT OF ERRORS IN ORIGINAL DATA

As stated earlier, the numerical values used in the foregoing computations have been obtained by approximations, and may be considerably in error. It is, therefore, desirable to know what effect errors in the various original data have on the final results.

The curves in figure 2 indicate the values of natural and fishing mortality which will be obtained with values of effort ratio and total mortality centering about those used in the foregoing computations. It will be noted that the effect of a given deviation is always greatest on natural mortality, and least on fishing mortality, in the second period. This is favorable to the practical application of the computations, since the rate of natural mortality, in itself, is of relatively minor importance in settling questions relating to the commercial fishery. On the other hand, rate of fishing mortality under current conditions (second period) of exploitation is of the greatest interest, since it leads to the estimation of the size of the stock of pilchards from which the commercial fishery must take its catch.

Considering the relative seriousness of various types of errors, it is apparent from figure 2 that errors in computation of total mortality are more serious than those in the effort ratio. For instance, the value of the effort ratio used in our computations was 4.0. From figure 2 it may be seen that, using total mortalities of .40 the first period and .80 the second period, a change in effort ratio from 4.0 to 3.5, a decrease of 12.5 percent, would cause an increase in the computed fishing mortality for the second period of only 1.9 percent (from .77 to .785). However, retaining the effort ratio of 4.0 and changing the total mortality for the first period from .40 to .35, again a decrease of 12.5 percent, would result in an increase in fishing mortality for the second period of 2.6 percent (from .77 to .79). In other words, a given percentage error in total mortality would produce about 1.4 times the effect on computed fishing mortality as the same percentage error in effort ratio (for the example given).

In general it may be said that fairly large errors in effort ratio would not seriously affect the results of the computations, provided that

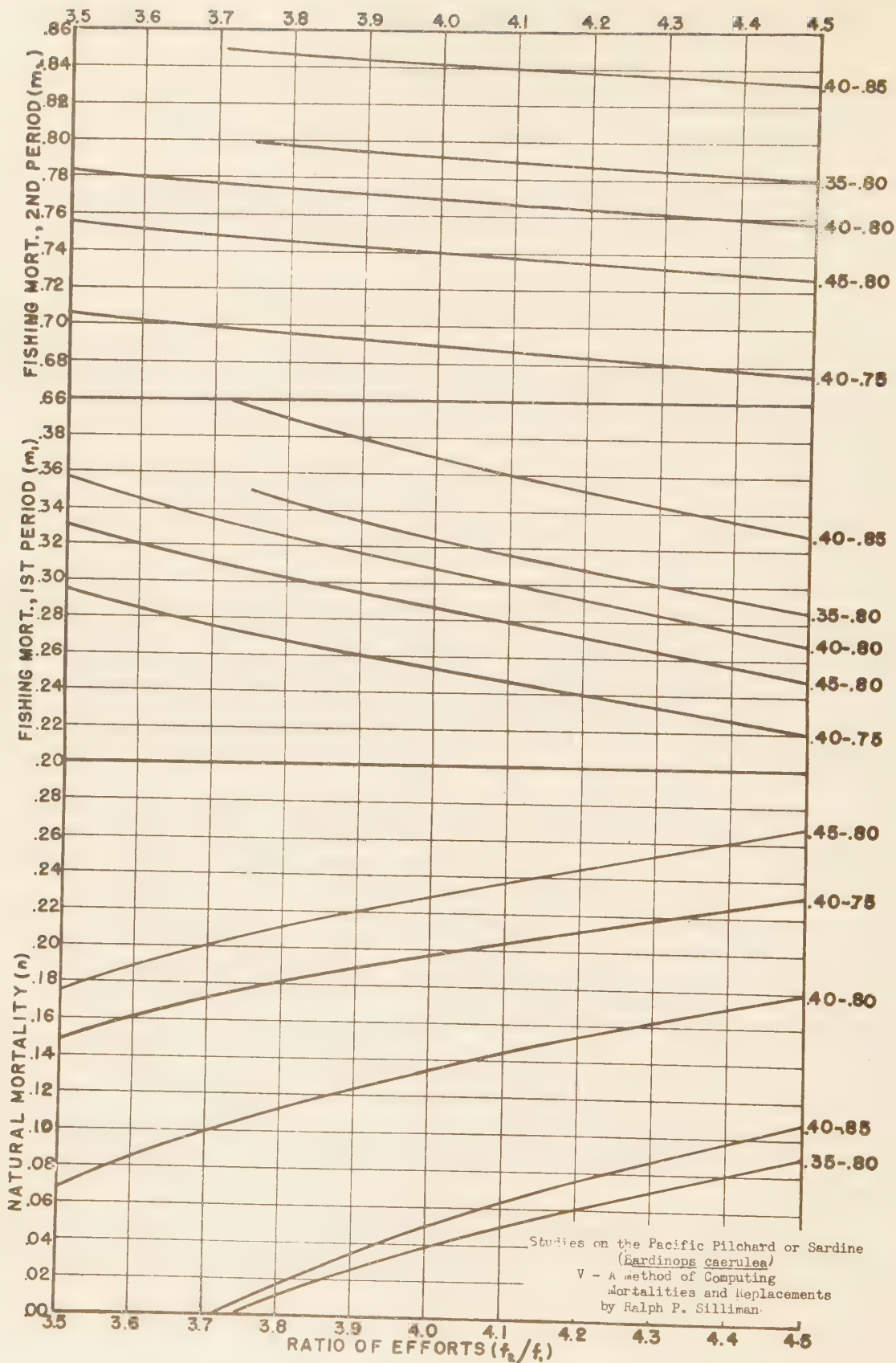


Figure 2. Natural and fishing mortalities for various combinations of effort ratio and total mortalities. Total mortalities for the first and second period respectively are given at the right-hand end of each curve.

the estimates of total mortality were accurate. On the other hand, a relatively small error in computed total mortality might cause errors great enough seriously to affect the final interpretation of the results. Thus it will be desirable, in the more precise determinations to be made in the future, to place special emphasis on accuracy in computing total mortality.

SUMMARY

1. If it is assumed for a given population that fishing effort is uniformly distributed, and that instantaneous competition between units of gear is absent, it is possible to estimate natural mortality, fishing mortality, and rate of recruitment.

2. The source data required are: (1) Age composition of the commercial stock, (2) total catch per season, and (3) relative amount of effort expended per season. Each of these must be known for at least two periods during which the fishery was relatively stabilized.

3. Total mortality may be estimated directly from the age composition of the stock at any time after stabilization.

4. Natural mortality may be separated from fishing mortality by assuming various ratios between the fishing mortalities for the two periods, and making successive trials until a combination giving the known ratios between the amounts of effort for the two periods is found.

5. Rate of recruitment may be estimated by extrapolating the natural and fishing mortality rates from the first fully available age class to the entering age class.

6. Errors in the source data will affect the estimate of natural mortality the most seriously, and the estimate of fishing mortality during the second period the least seriously.

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6. Thermal and Diurnal Changes in the Vertical Distribution of Eggs and Larvae

By

Ralph P. Silliman

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¹/ This report, without appendix A, was originally published in Sears Foundation: Journal of Marine Research, Vol. V, No. 2, under the title, "Thermal and Diurnal Changes in the Vertical Distribution of Eggs and Larvae of the Pilchard (Sardinops caerulea).²" It is reproduced by permission of the editors of that publication.

The original data used were collected as part of a joint program of oceanographic research carried on by the United States Fish and Wildlife Service and the Scripps Institute of Oceanography. Mr. O. E. Sette, then in charge of the South Pacific Investigation of the Fish and Wildlife Service suggested the investigation of the particular problems discussed in this report, and gave much helpful advice. Sorting of the plankton collections was accomplished with the assistance of Works Progress Administration projects Nos. 10917 and 65-2-08-286.

INTRODUCTION

Knowledge of the vertical distribution of pilchard eggs and larvae is of interest from two standpoints: first, in adding to the general knowledge of the early life of this species in the sea; and second, in defining the vertical range of its early stages so that regular surveys of the spawning grounds may be designed to sample all strata in which eggs and larvae are to be found. In reference to the second point it was desired, if possible, to relate vertical distribution to physical characteristics of the sea, so that the depth to which nets must be sent might be predicted. It was felt that the concentration of organisms at a given depth would be controlled chiefly by temperature, density, and light intensity. The analyses described in this paper have been designed to discover and define the relationships between these three variables and the vertical distribution of pilchard eggs and larvae.

METHODS

The field technique employed throughout the experiment was to make at each station successive net hauls, each sampling a layer of water below that of the preceding haul. In 1939, hauls were approximately horizontal. In 1941, however, oblique hauls were adopted to preclude the possibility of missing concentrations of larvae in the gaps between hauls. Each oblique haul extended diagonally from the top of the layer to be sampled by the next haul, to the bottom of the layer sampled by the preceding haul. The "surface" haul was made with an open net, while for the others the net was lowered closed to the desired level, hauled for from 15 to 20 minutes, closed, and brought to the surface.

Closing nets used were identical, except for dimensions and materials, with the one described by Leavitt (1935), and the tripping device was the one figured by him in a later paper (Leavitt, 1938, fig. 2). Sizes of nets and materials used are given in the list of stations at the end of this paper.

Temperatures were taken in 1939 with reversing thermometers, and in 1941 with a bourdon-type bathythermograph modified from the one described by Spilhaus (1940).

Water flow was measured in the 1939 hauls by a meter consisting of an impellor and counter. "Stray angle" (departure of the towing wire from the vertical) was measured with a pendulum protractor.

PERIOD AND AREA COVERED

Stations were located within a radius of 120 miles of San Diego, California, and were in an area somewhat to the south and east of the areas of heaviest pilchard spawning as indicated by other surveys. Four series of hauls were made in April, 1939, and seven in April, May, and June, 1941. Exact locations, dates, and depths fished are given in the list at the end of the paper.

CLASSIFICATION OF MATERIAL

Eggs and larvae were of course treated separately. Also, to take account of the fact that motility increases with size of larvae, these were divided into two categories: "large" and "small". A dividing line of 8 mm. had previously been used in other work, with which it was desired to compare the results of this analysis. Since this line did not split a mode in the length frequency distribution of larvae in the vertical serial hauls, it was retained for the present study.

Some larvae of the "small" group were lost through the meshes of the one-meter nets used. This, however, does not necessarily invalidate comparisons between numbers caught at different levels with the same net, since the loss should be a constant percentage of the total number caught.

STANDARDIZATION OF HAULS

Because of unavoidable variations in the speed of the ship and time of hauling, the amount of water strained by the net varied from haul to haul, even within a single series. These variations were discounted by putting all the hauls in each series on the basis of a standard volume of water strained. For the 1939 hauls, flow of water through the nets was measured directly by a current meter, but for the 1941 hauls, the relative amount was computed from the formula $\frac{W_1}{W_2} = \frac{\tan \angle 1}{\tan \angle 2}$, where $\frac{W_1}{W_2}$ = the ratio between the amounts of water strained for any two hauls, and $\angle 1$ and $\angle 2$ = their respective stray angles. Actual volumes of water strained averaged around 400 cubic meters for the one-meter nets, and 100 cubic meters for the half-meter nets. The numbers of organisms in the hauls were multiplied by factors $\frac{V_s}{V_h}$, where V_s = standard volume of water and V_h = volume strained in given haul) which made the numbers the same as if the standard volume of water had been strained, and had contained the same concentration of organisms as the water actually strained.

Because of the great range in numbers of organisms (from 6 to 6,000 in a single series of hauls) they could not be represented graphically on the same scale. Since the change in concentration from one series to another was not of interest, but only the changes from haul to haul within a series, the graphing difficulty was overcome by representing each vertical series by a polygon of equal area. To do this, the product of numbers of organisms by thickness of layer sampled was obtained for each haul. These products were summed for each station, and the original counts of organisms were multiplied by factors which made the sum of such products a constant for all stations. Besides overcoming the graphing difficulty, this computation placed the numbers at each level for all of the stations on a comparable basis, permitting direct comparison of catches at different levels even though they were not taken at the same station.

To avoid excessive random variability from small numbers, series containing less than 100 eggs, 50 small larvae, or 5 large larvae, were omitted from the analysis.

In order to construct the polygons mentioned above, it was necessary to compute the average depth for each haul. For the 1939 hauls, when the stray angle was measured two or three times during a haul, the angles were simply averaged and the depth computed from the average angle and the length of the towing wire. In 1941, when angles were measured each minute during a haul, it was possible to construct a plot of the course of each haul, (fig. 1). Average depths were computed from the plots by measuring the area bounded by each one and its baseline, and dividing by the length of the baseline.

EFFECT OF TEMPERATURE

Inspection of the vertical profiles for relative numbers of eggs and larvae, together with the corresponding temperature profiles (fig. 2) indicates a possible relationship between temperature and vertical distribution. Such a relationship could arise as the result of the seeking of an optimum temperature by the larvae, and by the adult fish which lay the eggs. Since pelagic fish eggs tend to remain in water of the same specific gravity as that in which they were fertilized (Walford, 1939), the vertical distribution of eggs should tend to reflect that of the parent fish at the time of spawning. This relationship is complicated by vertical turbulence above the thermocline, which tends to disperse passive bodies like fish eggs.

Whatever the nature of the relationship between temperature and the distribution of pilchard eggs, the larvae may be expected to respond directly to changes in temperature, since they are capable of locomotion. Again the relationship is probably complicated by other factors, such as the amount of fodder organisms present.

To measure the correlation between temperature and concentrations of eggs and larvae, the relative numbers were plotted as regressions on degrees centigrade (fig. 3). Hauls above a depth of 10 meters were omitted because of the reversals in egg and larvae profiles which often occurred in that layer. Also excluded were zero hauls below the first. Inclusion of either of these two categories of hauls would obscure the decrease from the maximum concentrations down to zero, which is the point of chief interest in the regressions in so far as they are to be used in determining the depth of net hauls for regular surveys. Correlation coefficients were .590 for eggs, .557 for small larvae, and .548 for large larvae, corresponding to probabilities of .010, .041, and .024 of chance occurrence. Combining these probabilities by the method of Fisher (1936, p. 105) indicates that the result, as a whole, is highly significant ($P = .0009$).

Of special interest in the foregoing correlations are the intersections of the computed regression lines with their baselines, since these should indicate the temperature below which we would not expect to find eggs or larvae. The indicated minimum temperatures are 10.5° for eggs, 12.4° for small larvae, and 12.0° for large larvae. Since the regressions for large and small larvae were found by Fisher's (1936 p. 146) "t" test not to differ significantly in slope, they were combined, giving an indicated minimum of 12.0° for both size categories.

DIURNAL CHANGES

To determine the extent and nature of diurnal changes in the vertical distribution of pilchard larvae, two special pairs of serial hauls were run in June, 1941, the first of each pair being occupied around midnight, and the other around noon. Due to unavoidable movements of the vessel the two members of each pair were not located at exactly the same point geographically, but approximately the same position was maintained and they were probably in water of similar characteristics.

One of the chief differences between the night and day hauls was that the former contained many more large larvae than the latter (fig. 4). This could result from any one of three causes: (1) location of the day hauls in an area of lesser concentration than the night hauls, as a result of movement of the ship through the water between the two series; (2) migration of most of the larvae below the levels fished, during the daytime; (3) dodging of the net by the larvae, in the daytime.

The first explanation is a highly improbable one, since the larger catches at night have been observed many times previously, for other plankton organisms and larvae of other species of fish. Also, our regular surveys of the spawning grounds show the night catches of larvae to be consistently larger than the day.

The second explanation has been most widely entertained by others investigating vertical migrations. For instance, it was advanced by E. S. Russel (1928) to explain the larger catches of clupeoid and gobioid larvae at night, but he was later forced to abandon it when subsequent daylight hauls near the bottom (Russel, 1930) did not average larger catches than the ones in the upper layers of water. For our own data, the taking of at least two blank hauls (fig. 4) below those which contained any larvae, argues against the probability of a concentration of larvae below the levels sampled.

Elimination of the first two explanations leaves only the third - dodging of the net in the daytime. Russel (1926) and Johansen (1925) admit this possibility, but doubt that fish larvae could swim fast enough for successful dodging. On this point it may be well to consider how fast it would be necessary for larvae to swim in order to get out of the way of the net. All nets towed in the conventional manner give warning of their approach by means of the piece of line which attaches them to the towing wire. In our gear this line was about 5 meters long, while our average speed of towing was around 50 cm. per second. The larvae would thus have about 10 seconds to swim out of the way. Since the maximum distance they would have to swim would be the radius of the net, or 50 cm., a swimming rate of 5 cm. per second would be sufficient if the direction of swimming were favorable. This does not seem an incredible rate for pilchard larvae of the size in question (over 8 mm. in length). Likewise it does not seem unreasonable that they should swim away from the center of disturbance, and therefore in a direction favorable to escape from the oncoming net.

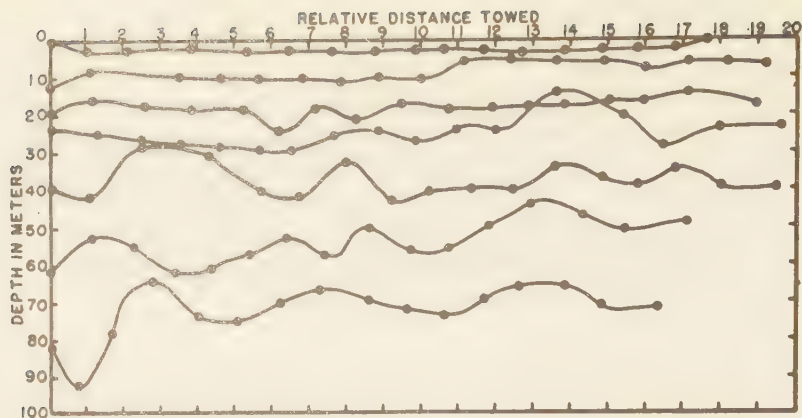


Figure 1. Course of serial hauls for a typical station (No. 2046). "Relative distance was computed from the product of time and average tangent of angle of stray for each one-minute interval of the hauls. Depths were computed from cosine of angle of stray.

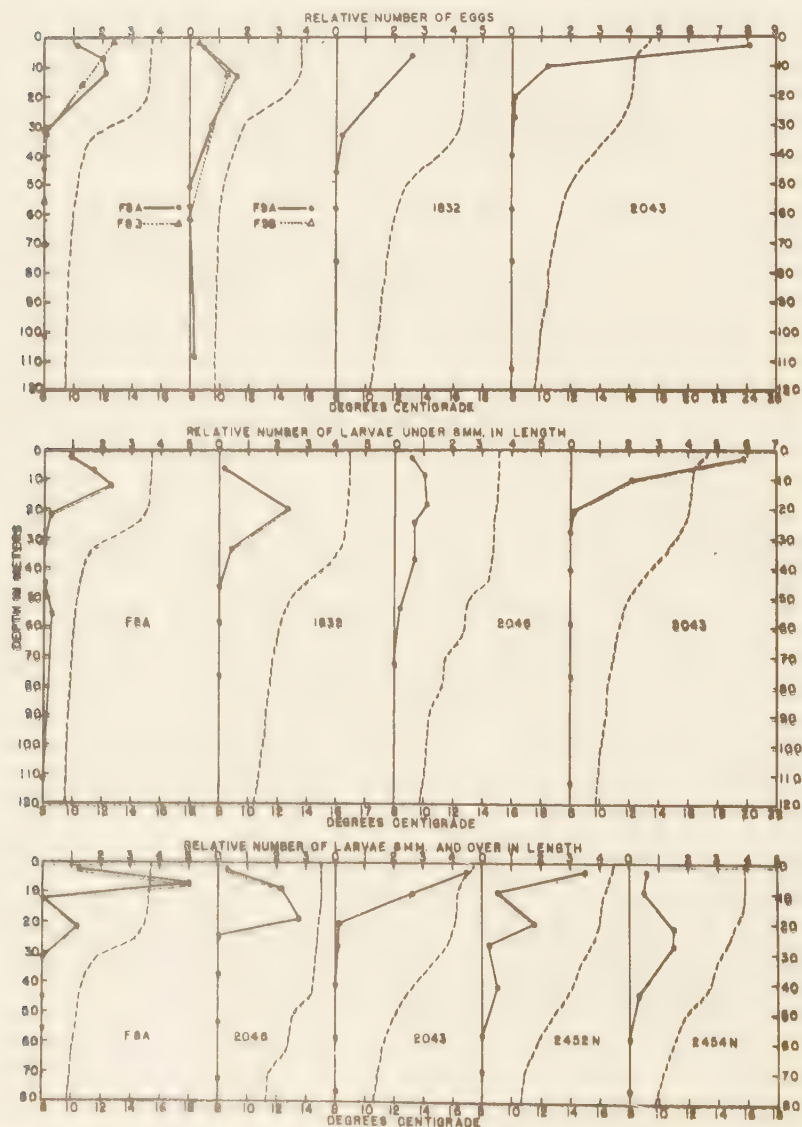


Figure 2. Relative numbers of eggs and larvae taken at each depth. Broken line shows temperature. For the large larvae two series taken around noon have been omitted because of the effect of light. They are shown in figure 4.

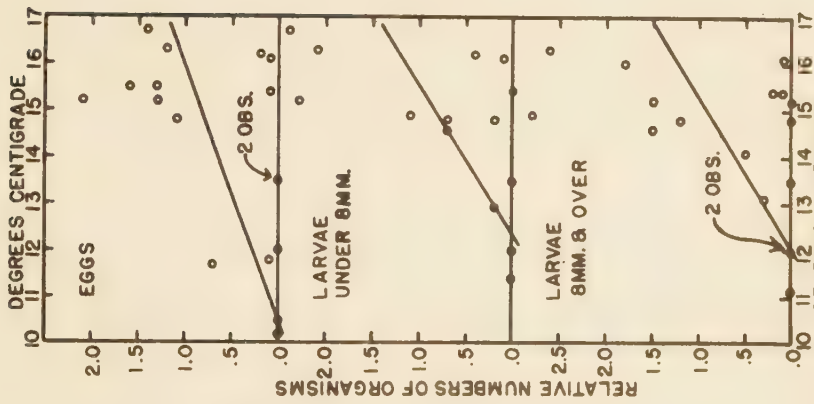


Figure 3. Regressions of numbers of eggs and larvae on temperature. Lines shown are "least squares fits"

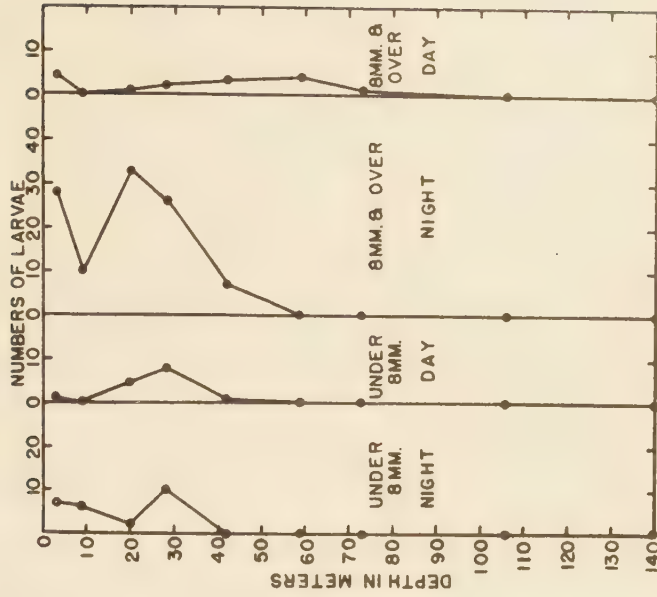


Figure 4. The combined catches of stations 2452 and 2454, comparing day and night hauls at each depth. Numbers represent actual numbers caught.

In the day hauls the large larvae were not only less numerous than in the night hauls, but also appeared to be distributed in somewhat deeper levels. A greater relative number of larvae at the deeper levels in the daytime than at night might result from more successful dodging of the net in the better illuminated upper layers of water. A greater absolute number, however, could result only from downward migration in the daytime, providing the overall concentration were not greater. Such a downward migration might well occur as a result of negative phototropism. Comparison of the night and day hauls for stations 2452 and 2454 (fig. 4) reveals that there actually were more larvae at the deeper levels in the day hauls. Four larvae were taken in the day series at 59 meters, and one at 73 meters, while none were taken at either of these levels in the night series. The significance of these differences was tested by means of Bayes' theorem, (using the formulation of Pearson, 1930, page lxx) considering a success, the presence of a larva at the indicated depth, and assuming the same overall concentration for day and night (in other words assuming that the lesser numbers in the upper layers in the daytime were due to dodging of the net). The computation gave values of P of .06 at 59 meters and .50 at 73 meters. The latter, of course, does not indicate a significant difference between day and night hauls, but the former, closely approaching the conventional significance level of .05, gives some indication of an actually deeper distribution in the daytime.

In applying this result to the prediction of vertical distribution, a knowledge of the penetration of light at various times of day is necessary. Unfortunately, no empirical data for the area of our survey are available, and we are forced to argue by analogy with data collected elsewhere. G. L. Clarke (1934) has shown in his graphs that submarine irradiation in the Atlantic Ocean reaches nearly its maximum value shortly after sunrise, and is maintained there until shortly before sunset. Accordingly, extension of the regular hauls below 73 meters between sunrise and sunset would seem to be necessary in order to make sure of sampling all strata in which larvae were to be found.

SUMMARY AND CONCLUSIONS

Analysis of catches of pilchard eggs and larvae taken in serial hauls in 1939 and 1941 indicates the following relationships and effects:

1. A positive correlation of concentrations of eggs and larvae with temperature, at least within the range of 10° to 17° C.
2. An apparent dodging of the nets by the larger larvae, in the layers of water which are illuminated in the daytime.
3. A negative phototropism for the larger larvae.

Such relationships with physical conditions as have been indicated by the present study may, of course, hold true only for the particular set of oceanographic conditions prevailing at the times and places where the data were gathered. For instance, the relationship between the horizontal distribution of pilchard eggs and temperature as indicated by our regular spawning surveys for 1941 was quite different from that found in 1940.

However, the data for the present study were gathered in two different years (1939 and 1941) and over a considerable area, so that they may permit of some generalization.

It may have been noted that the concentrations of eggs and larvae are correlated with depth as well as temperature, since the latter two are themselves highly correlated. However, there are some instances where the deeper extension of warm water corresponds with a deeper distribution of eggs or larvae (cf. fig. 2). Also, there is some logical basis for a correlation with temperature, which might act either as the cause of direct reaction of the larvae, or as an indicator of density differences affecting the distribution of eggs.

It is not intended to argue that temperature itself necessarily controls the vertical distribution of pilchard eggs and larvae. Their location may be determined by complex reactions of the spawners to a combination of physical conditions, including salinity, food, density, etc. To the extent that these would induce spawning in a homologous portion of the layer of water above the thermocline, temperature may be merely an indicator and not a cause. This, of course, does not detract from the usefulness of temperature as a guide to vertical distribution.

As a basis for predicting the proper depths to which to send nets on regular surveys, the regressions of egg and larvae concentrations on temperature indicate that hauls should be made deep enough to go below temperatures of 10.5° C. for eggs and 12.0° for larvae. Distribution of the large larvae during the daytime shows the need for fishing to a depth greater than 73 meters between sunrise and sunset.

A P P E N D I X A

TABLES OF DETAILED TOWING DATA

Explanation of tables: The hauls at each station and the observations during each haul are arranged chronologically and numbered consecutively, beginning with one. Time is ship's time, with hours numbered from 1 for 1 a.m. to 24 for midnight. Meters of wire out (m. out) refers to the length of towing wire from the surface of the sea to the point of attachment of the net. The stray angle ($^{\circ}/$) is the departure of the towing wire from the vertical, expressed in degrees. A dash (-) represents a missing observation.

Table 1.--Towing data for Station F8A, April 19, 1939.

(See page 6 for explanation.)

Observation number	Haul number							
	1	2	3	4	5	6	7	8
	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.
	Time:out	Time:out	Time:out	Time:out	Time:out	Time:out	Time:out	Time:out
1	3:25	4:15	4:46	5:14	5:51	6:30	7:16	9:24
2	3:41	4:16	4:47	5:15	5:52	6:40	7:17	9:48
3		4:20	4:50	5:17	5:57	6:42	7:21	9:60
4		4:25	4:56	5:22	6:01	6:32	7:27	9:43
5		4:29	5:01	5:29	6:08	6:45	7:32	9:48
6		4:30						

Table 2.--Towing data for Station F8B, April 19, 1939.

(See page 6 for explanation.)

Observation number	Haul number			
	1	2	3	4
	m.o.	m.o.	m.o.	m.o.
	Time:out	Time:out	Time:out	Time:out
1	15:18	15:44	16:12	16:44
2		15:52	16:20	16:45
3		15:59	16:28	16:50
4				17:02
5				

Table 3.--Towing data for Station F9A, April 20, 1939.

(See page 6 for explanation.)

Observation number	Haul number				
	1	2	3	4	5
	m.o.	m.o.	m.o.	m.o.	m.o.
	Time:out	Time:out	Time:out	Time:out	Time:out
1	2:20	2:51	4:03	4:53	5:37
2	2:37	2:53	4:05	4:56	5:40
3		2:59	4:15	5:08	5:49
4		3:09	4:21	5:14	5:52

Table 4.--Towing data for Station F9B, April 20, 1939. (See page 6 for explanation.)

Observation number	Haul number							
	1	2	3	4	5	6	7	8
	m. out	m. out	m. out	m. out	m. out	m. out	m. out	m. out
	Time	Time	Time	Time	Time	Time	Time	Time
1	8:46:22	9:13:20	10:52:100	12:45:200				
2	8:57:22	9:17:20	10:53:100	12:46:200	51			
3		9:28:20	11:02:100	12:57:200	42			
4			11:09:100	13:02:200				

Table 5.--Towing data for Station 1832, April 10, 1941. (See page 6 for explanation.)

Observation number	Haul number											
	1	2	3	4	5	6	7	8	9	10	11	12
	m. out	m. out	m. out	m. out	m. out	m. out	m. out	m. out	m. out	m. out	m. out	m. out
	Time	Time	Time	Time	Time	Time	Time	Time	Time	Time	Time	Time
1	11:09:15	12:38:30	13:13:45	13:49:60	14:26:75	14:59:100	15:36					
2	11:11:14	12:40:29	13:15:44	13:51:59	14:28:74	15:01:98	15:38					
3	11:13:12	12:42:28	13:17:43	13:53:58	14:30:73	15:03:97	15:32					
4	11:15:10	12:44:27	13:19:42	13:55:57	14:32:72	15:05:96	15:30					
5	11:17:9	12:46:26	13:21:41	13:57:56	14:34:71	15:07:94	15:40					
6	11:19:8	12:48:25	13:23:40	13:59:55	14:36:70	15:09:92	15:28					
7	11:21:6	12:50:24	13:25:39	14:01:54	14:38:69	15:11:91	15:30					
8	11:23:4	12:52:23	13:27:38	14:03:53	14:40:68	15:13:90	15:28					
9	11:25:3	12:54:22	13:29:37	14:05:52	14:42:67	15:15:88	15:38					
10	11:27:2	12:56:21	13:31:36	14:07:51	14:43:66	15:17:86	15:32					
11	11:29:0	12:58:20	13:33:35	14:09:50	14:46:65	15:19:85	15:34					
12	11:30:0	13:01:20	13:34:35	14:10:50	14:47:65	15:20:85	15:35					

Table 6. --Towing data for Station 2046, April 30, 1941. (Continued from page 6 for explanation.)

Obs. rv. tion number	1		2		3		4		5		6		7	
	m.	s.	m.	s.	m.	s.	m.	s.	m.	s.	m.	s.	m.	s.
1	17:10:	0	42:17:53:	15	37:13:03:	25	41:18:38:	40	54:19:35:	60	48:20:09:	85	43:20:32:	110:45
2	17:11:	4	48:17:59:	15	57:18:09:	30	52:18:39:	40	-	19:36:60	45:20:09:	85	51:20:33:	110:35
3	17:12:	4	56:17:40:	15	50:18:10:	30	-	18:40:40	48:19:37:	60	52:20:06:	85	50:20:34:	110:45
4	17:13:	4	60:17:41:	15	47:18:11:	30	51:18:41:	40	45:19:38:	60	59:20:07:	85	43:20:39:	110:54
5	17:14:	4	49:17:42:	15	46:18:12:	30	35:18:42:	40	46:19:39:	60	48:20:08:	85	45:20:36:	110:47
6	17:15:	4	48:17:43:	15	50:18:13:	30	53:18:43:	40	44:19:40:	60	46:20:09:	85	47:20:37:	110:47
7	17:16:	4	49:17:44:	15	40:18:14:	30	43:18:44:	40	43:19:41:	60	57:20:10:	80	48:20:38:	105:48
8	17:17:	4	54:17:45:	15	52:18:15:	30	55:18:45:	40	52:19:42:	60	52:20:11:	80	44:20:39:	105:50
9	17:18:	4	34:17:46:	15	40:18:16:	30	50:18:46:	40	52:19:43:	60	48:20:12:	80	50:20:40:	105:48
10	17:19:	4	42:17:47:	10	54:18:17:	25	44:18:47:	35	40:19:44:	60	50:20:13:	80	45:20:41:	105:47
11	17:20:	4	48:17:48:	10	-	18:18:25	47:18:48:	35	48:19:45:	55	44:20:14:	80	46:20:42:	105:45
12	17:21:	4	47:17:49:	10	50:18:19:	25	44:18:49:	35	44:19:46:	55	52:20:15:	75	48:20:43:	100:46
13	17:22:	4	44:17:50:	10	54:18:20:	25	48:18:50:	35	66:19:47:	55	47:20:16:	75	54:20:44:	100:48
14	17:23:	4	46:17:51:	10	41:18:21:	25	46:18:51:	35	56:19:48:	55	45:20:17:	75	50:20:45:	100:48
15	17:24:	4	43:17:52:	10	52:18:22:	25	53:18:52:	35	36:19:49:	55	51:20:18:	75	47:20:46:	100:44
16	17:25:	4	47:17:53:	10	42:18:23:	25	45:18:53:	35	49:19:50:	55	44:20:19:	75	49:20:48:	100:-
17	17:26:	0	-	17:54:10	45:18:24:	25	-	18:54:35	-	19:51:55	-	-	-	-

Table 7.--Towing data for Station 2043, May 2, 1941. (See page 6 for explanation.)

Observation number		1		2		3		4		5		6		7		8	
		m.	s.	m.	s.	m.	s.	m.	s.	m.	s.	m.	s.	m.	s.	m.	s.
		Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out
1	19:58	0	39	20	30	15	33	20	58	30	30	21	24	40	50	21	51
2	19:59	4	35	20	31	15	49	20	59	30	46	21	25	40	49	21	52
3	20:00	4	47	20	32	15	30	21	00	30	39	21	26	40	40	21	53
4	20:02	4	27	20	33	15	35	21	01	30	38	21	27	40	35	21	54
5	20:03	4	45	20	34	15	43	21	02	30	41	21	28	40	47	21	55
6	20:04	4	45	20	35	15	43	21	03	30	41	21	29	40	41	21	56
7	20:05	4	34	20	36	15	43	21	04	30	45	21	30	40	36	21	57
8	20:06	4	22	20	37	15	44	21	05	30	42	21	31	40	39	21	58
9	20:07	4	30	20	38	15	43	21	06	30	40	21	32	40	43	21	59
10	20:08	4	38	20	39	10	38	21	07	25	37	21	33	35	44	22	00
11	20:09	4	35	20	40	10	43	21	08	25	38	21	34	35	36	22	01
12	20:10	4	38	20	41	10	34	21	09	25	41	21	35	35	35	22	02
13	20:11	4	37	20	42	10	45	21	10	25	41	21	36	35	43	22	03
14	20:12	4	46	20	43	10	42	21	11	25	40	21	37	35	44	22	04
15	20:13	0	-	20	44	10	24	21	12	25	44	21	38	35	39	22	05
16	:	:	20	45	10	:	45	21	13	25	48	21	39	35	42	22	06
17	:	:	20	46	10	-	21	14	25	-	21	40	35	-	22	08	55

Table 9.—Towing data for Station 2452D, June 13, 1941. (See page 6 for explanation.)

Observer:	Haul number	1		2		3		4		5		6		7		8		9	
		m.	o.	m.	o.	m.	o.	m.	o.	m.	o.	m.	o.	m.	o.	m.	o.	m.	o.
vation:		Time out:	L	Time out:	L	Time out:	L	Time out:	L	Time out:	L	Time out:	L	Time out:	L	Time out:	L	Time out:	L
number:																			
1	8:58:	0	37:9:35:15	39:10:05:30	51:10:35:40	25:11:05:60	45:11:38:85	45:12:14:10	45:13:02:160	19:13:43:210:42									
2	8:59:	4	33:9:36:15	41:10:06:30	46:10:36:40	30:11:06:60	45:11:39:85	50:12:15:10	46:13:03:160	41:13:44:210:48									
3	9:00:	4	38:9:37:15	45:10:07:30	45:10:37:40	40:11:07:60	44:11:40:85	47:12:16:10	46:13:04:160	51:13:45:210:48									
4	9:01:	4	40:9:38:15	44:10:08:30	50:10:38:40	47:11:08:60	46:11:41:85	41:12:17:10	45:13:05:160	53:13:46:210:46									
5	9:02:	4	38:9:39:15	50:10:09:30	54:10:39:40	44:11:09:60	45:11:42:85	40:12:18:10	48:13:06:160	47:13:47:210:46									
6	9:03:	4	45:9:40:15	43:10:10:30	45:10:40:40	35:11:10:60	47:11:43:85	38:12:19:10	49:13:07:160	46:13:48:210:48									
7	9:04:	4	44:9:41:15	40:10:11:30	42:10:41:40	42:11:11:60	46:11:44:85	43:12:20:105	47:13:08:150	43:13:49:200:50									
8	9:05:	4	35:9:42:15	41:10:12:30	43:10:42:40	47:11:12:60	45:11:45:80	43:12:21:105	44:13:09:150	44:13:50:200:51									
9	9:06:	4	40:9:43:15	42:10:13:30	50:10:43:40	40:11:13:60	44:11:46:80	43:12:22:105	48:13:10:150	46:13:51:200:47									
10	9:07:	4	45:9:44:10	34:10:14:25	46:10:44:40	34:11:14:55	44:11:47:80	41:12:23:105	50:13:11:150	46:13:52:200:47									
11	9:08:	4	42:9:45:10	41:10:15:25	41:10:45:40	37:11:15:55	47:11:48:80	44:12:24:105	49:13:12:150	45:13:53:200:47									
12	9:09:	4	42:9:46:10	53:10:16:25	44:10:46:40	45:11:16:55	45:11:49:75	41:12:25:105	45:13:13:140	45:13:54:190:46									
13	9:10:	4	43:9:47:10	43:10:17:25	56:10:47:35	44:11:17:55	47:11:50:75	42:12:26:100	47:13:14:140	46:13:55:190:48									
14	9:11:	4	45:9:48:10	40:10:18:25	51:10:48:35	39:11:18:55	45:11:51:75	45:12:27:100	45:13:15:140	47:13:56:190:45									
15	9:12:	4	45:9:49:10	51:10:19:25	43:10:49:35	39:11:19:55	43:11:52:75	46:12:28:100	45:13:16:140	45:13:57:190:45									
16	9:13:	4	35:9:50:10	46:10:20:25	37:10:50:35	40:11:20:55	43:11:53:75	46:12:29:100	46:13:17:140	46:13:58:190:47									
17	9:14:	0	9:51:10	44:10:21:25	42:10:51:35	39:11:21:55	44:11:56:75	12:30:100	46:13:19:140	38:14:00:190:37									
18	:	:	9:52:10	10:22:25	10:53:35	11:23:55	:	12:32:100	36:	:	:								

Table 10.---Towing data for Station 2454N, June 18-19, 1941. (See page 6 for explanation.)

Observer:	Haul number								
	1	2	3	4	5	6	7	8	9
number:	m.:o	m.:o	m.:o	m.:o	m.:o	m.:o	m.:o	m.:o	m.:o
Time out:	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out	Time out
Time in:	Time in	Time in	Time in	Time in	Time in	Time in	Time in	Time in	Time in
1	0:50:21:37	1:15:37	22:06:30:40	22:39:40:37	23:12:50:30	23:44:55:42	24:20:11:10	24:59:16:21	1:39:21:38
2	4:15:21:38	1:15:35	22:09:30:40	22:40:40:40	23:13:50:37	23:45:55:45	24:21:11:35	1:00:16:45	1:40:21:38
3	4:23:21:39	1:15:30	22:10:30:42	22:41:40:40	23:14:50:45	23:45:55:44	24:22:11:44	1:01:16:47	1:41:21:52
4	4:34:21:40	1:15:45	22:11:30:38	22:42:40:40	23:15:50:50	23:47:55:37	24:23:11:45	1:02:16:44	1:42:21:54
5	4:35:21:41	1:15:42	22:12:30:38	22:43:40:42	23:16:50:46	23:48:55:36	24:24:11:40	1:03:16:42	1:43:21:46
6	4:35:21:42	1:15:43	22:13:30:35	22:44:40:42	23:17:50:36	23:49:55:38	24:25:11:46	1:04:16:45	1:44:21:46
7	4:40:21:43	1:15:34	22:14:30:36	22:45:40:44	23:18:50:30	23:50:58:42	24:26:10:45	1:05:15:47	1:45:20:46
8	4:50:21:44	1:15:35	22:15:30:37	22:46:40:45	23:19:50:33	23:51:58:47	24:27:10:47	1:06:15:47	1:45:20:48
9	4:41:21:45	1:15:42	22:16:30:42	22:47:40:45	23:20:50:40	23:52:58:50	24:28:10:46	1:07:15:45	1:47:20:41
10	4:43:21:46	1:10:37	22:17:25:33	22:48:46:35	23:21:55:43	23:53:58:47	24:29:10:40	1:08:15:44	1:48:20:36
11	4:43:21:47	1:10:40	22:18:25:30	22:49:35:45	23:22:55:37	23:54:58:45	24:30:10:35	1:09:15:45	1:49:20:38
12	4:37:21:46	1:10:42	22:19:25:35	22:50:35:46	23:23:55:33	23:55:57:44	24:31:10:43	1:10:14:40	1:50:19:42
13	4:40:21:49	1:10:45	22:20:25:40	22:51:35:46	23:24:55:33	23:56:57:42	24:32:10:47	1:11:14:41	1:51:19:44
14	4:44:21:50	1:10:30	22:21:25:40	22:52:35:42	23:25:55:44	23:57:57:40	24:33:10:43	1:12:14:50	1:52:19:50
15	4:43:21:51	1:10:42	22:22:25:42	22:53:35:42	23:26:55:44	23:58:57:43	24:34:10:45	1:13:14:47	1:53:19:46
16	4:43:21:52	1:10:40	22:23:25:40	22:54:35:45	23:27:55:40	23:59:57:40	24:35:10:49	1:14:14:44	1:54:19:44
17	4:43:21:53	1:10:44	22:24:25:44	22:55:35:46	23:28:55:44	24:00:57:39	24:36:10:20	1:15:14:40	1:55:19:16
18	4:43:21:54	1:10:40	22:25:25:43	22:56:35:46	23:30:55:46				

Table 11.—Towing data for Station 2454D, June 19, 1941. (See page 6 for explanation.)

Observer:	Haul number											
Station:	1	2	3	4	5	6	7	8	9			
Number:	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.	m.o.
	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:	Time out:
1	:8:26:0	:30:8:50	:15:20:9	:16:30:32	:9:43:40	:25:10:10	:16:40:10	:37:85:40	:11:09:11	:48:11:44	:160:41:12	:28:210:19
2	:8:27:4	:38:8:51	:15:32:9	:17:30:44	:9:44:40	:35:10:11	:16:45:10	:38:85:42	:11:10:11	:49:11:45	:160:44:12	:29:210:26
3	:8:28:4	:50:8:52	:15:48:9	:18:30:50	:9:45:40	:52:10:12	:16:43:10	:39:85:45	:11:11:11	:46:11:46	:160:45:12	:30:210:38
4	:8:29:4	:42:8:53	:15:44:9	:19:30:42	:9:46:40	:40:10:13	:16:41:10	:40:85:42	:11:12:11	:45:11:47	:160:46:12	:31:210:38
5	:8:30:4	:44:8:54	:15:40:9	:20:30:34	:9:47:40	:30:10:14	:16:45:10	:41:85:36	:11:13:11	:45:11:48	:160:45:12	:32:210:43
6	:8:31:4	:46:8:55	:15:44:9	:21:30:32	:9:48:40	:40:10:15	:16:43:10	:42:85:38	:11:14:11	:49:11:49	:160:47:12	:33:210:42
7	:8:32:4	:42:8:56	:15:45:9	:22:30:40	:9:49:40	:43:10:16	:16:38:10	:43:80:42	:11:15:11	:45:11:50	:150:43:12	:34:200:44
8	:8:33:4	:44:8:57	:15:40:9	:23:30:45	:9:50:40	:45:10:17	:16:42:10	:44:80:46	:11:16:11	:51:11:51	:150:43:12	:35:200:47
9	:8:34:4	:44:8:58	:15:42:9	:24:30:45	:9:51:40	:44:10:18	:16:45:10	:45:80:44	:11:17:11	:53:11:52	:150:40:12	:36:200:52
10	:8:35:4	:42:8:59	:10:44:9	:25:25:35	:9:52:35	:35:10:19	:16:55:47	:46:80:40	:11:18:11	:53:11:53	:150:40:12	:37:200:49
11	:8:36:4	:35:9:00	:10:45:9	:26:25:45	:9:53:35	:45:10:20	:16:55:49	:47:80:38	:11:19:11	:54:11:54	:150:42:12	:38:200:51
12	:8:37:4	:43:9:01	:10:47:9	:27:25:47	:9:54:35	:48:10:21	:16:55:46	:48:80:44	:11:20:11	:55:11:55	:140:43:12	:39:190:51
13	:8:38:4	:44:9:02	:10:45:9	:28:25:44	:9:55:35	:48:10:22	:16:55:38	:49:75:45	:11:21:11	:56:11:56	:140:45:12	:40:190:43
14	:8:39:4	:37:9:03	:10:42:9	:29:25:43	:9:56:35	:47:10:23	:16:55:35	:50:75:42	:11:22:11	:57:11:57	:140:41:12	:41:190:40
15	:8:40:4	:45:9:04	:10:45:9	:30:25:40	:9:57:35	:44:10:24	:16:55:34	:51:75:36	:11:23:11	:58:11:58	:140:44:12	:42:190:40
16	:8:41:0	--	:9:05:10	:46:9:31	:25:32:9	:58:35:38	:10:25:55	:45:10:52	:75:33:11	:24:100:40	:11:59:140:41	:12:43:190:49
17	:	:9:06:10	:47:9:32	:25:33:9	:59:35:32	:10:26:55	:42:10:53	:75:46:11	:26:100:46	:12:02:140:35	:12:45:190:33	:
18	:	:9:07:10	:47:9:34	:25:34:10	:00:35:40	:10:27:55	:37:	:	:	:	:	:

APPENDIX B

LISTS SHOWING TIME AND LOCATION OF HAULS, DEPTHS FISHED, AND NUMBERS OF EGGS AND LARVAE TAKEN

Data are given in the following order: Station number; date; time interval; latitude; longitude; type of net; depth interval for each haul; numbers of eggs; length and number of larvae for larvae of each .5 mm. interval of length. Time of day is given to the nearest hour with the hours numbered consecutively from 1 for 1 a.m. to 24 for midnight. Depths are in meters and lengths of larvae in millimeters.

Example: (Station) 1832; (Month) 4/ (Day) 10/ (Year) 41; (Start) 11h- (End) 15h; (North latitude) 33:13; (West longitude) 118:26; (Type of net) B; (Upper limit of stratum fished, depth) 0- (Lower limit of stratum fished, depth) 13; (Number of eggs taken) E 181; (Larvae) L: (Length) 2.5, (Number) 3; (Length) 3.0, (Number) 35; (length) 3.5, (Number) 4; (Limits) 17-26; (Number of eggs) E 103; (Larvae) L: (Length) 2.5, (Number) 22; (Length) 3.0, (Number) 366; etc.

Net types are as follows: Type A is a closing net of one meter diameter mouth; made of No. 24XXX grit gauze, with the last half meter of No. 56XXX grit gauze; and with a detachable "cod end" of No. 56XXX grit gauze. Type B is a closing net of one-half meter diameter mouth; made of No. 40XXX grit gauze, with the last 65cm. of No. 56XXX grit gauze. Type C is a closing net of one meter diameter of mouth; made of cotton scrim with openings approximately 1 mm. square, with the last half meter of No. 56XXX grit gauze; and with detachable "cod end" of No. 56XXX grit gauze. Approximate sizes of openings of XXX grit gauzes are: No. 24, 1.10 mm.; No. 40, .65 mm.; No. 56, .47 mm.

F8A; 4/19/39; 3h-9h; 32:48, 117:42; A; 0-3: E 1877; L: 4.0, 1; 4.5, 1; 5.0, 4; 5.5, 2; 7.0, 2; 8.0, 1; 9.5, 1; 6-8: E 2879; L: 4.0, 1; 4.5, 3; 5.0, 7; 6.0, 1; 6.5, 2; 7.0, 1; 7.5, 1; 8.0, 2; 9.0, 2; 10.0, 1; 10.5, 1; 7-16: E 3878; L: 3.0, 2; 3.5, 1; 4.0, 3; 4.5, 8; 5.0, 9; 5.5, 2; 6.0, 2; 17:25: E 1265; L: 5.0, 1; 8.0, 1; 30-34: E 56; L: 0; 44-46: E 5; L: 0; 45-60: E 0; L: 4.5, 2; 108-115: E 6; L: 0.

F8B; 4/19/39; 15h-19h; 32:48, 117:44; A; 0-2: E 2892; L: 5.5, 1; 6.5, 1; 7.0, 1; 15-17: E 1359; L: 3.5, 1; 4.5, 1; 29-35: E 88; L: 0; 53-58: E 8; L: 0; 68-72: E 0; L: 0; 164-183: E 4; L: 0.

F9A; 4/20/39; 2h-8h; 32:30, 117:32; A; 0-5: E 52; L: 3.5, 6; 4.0, 1; 4.5, 2; 5.0, 4; 5.5, 6; 6.0, 1; 6.5, 3; 7.0, 2; 12-14: E 194; L: 6.0, 1; 28-32: E 54; L: 0; 45-57: E 1; L: 6.0, 1; 56-59: E 1; L: 0; 109-*: E 7; L: 0.

F9B; 4/20/39; 9h-13h; 32:29, 117:39; A; 0-2: E 940; L: 5.5, 2; 6.0, 4; 6.5, 5; 7.0, 7; 8.0, 3; 8.5, 1; 9.0, 1; 9.5, 2; 10.0, 1; 11.0, 1; 14-*: E 4137; L: 3.5, 1; 4.0, 6; 5.0, 1; 6.0, 1; 57-66: E 6; L: 0; 126-149: E 4; L: 0.

*Only one stray angle reading.

1832; 4/10/41; 11h-15h; 33:13, 118:26; B; 0-13: E 181; L: 2.5,3; 3.0,35;
3.5,4; 17-26: E 103; L: 2.5,22; 3.0,366; 3.5,187; 4.0,2; 4.5,6; 5.5,1;
28-39: E 11; L: 2.5,1; 3.0,47; 3.5,31; 4.0,2; 4.5,6; 5.0,2; 41-55: E 0;
L: 0; 53-66: E 0; L: 3.0,2; 3.5,2; 69-83: E 0; L: 2.5,1; 3.5,1; 5.0,1.

2046; 4/30/41; 17h-21h; 32:29, 119:26; B; 0-3: E 0; L: 3.0, 3; 3.5,3;
4.0,1; 4.5,2; 5.0,33; 5.5,36; 6.0,9; 6.5,1; 7.0,1; 9.5,1; 6-12: E 0; L:
3.5,2; 4.0,2; 4.5,2; 5.0,31; 5.5,51; 6.0,55; 6.5,20; 7.0,3; 7.5,4; 8.0,2;
8.5,2; 9.0,1; 9.5,1; 10.0,2; 11.0,1; 15-25: E 0; L: 2.5,1; 3.0,1; 3.5,2;
4.0,1; 4.5,3; 5.0,27; 5.5,37; 6.0,74; 6.5,23; 7.0,9; 7.5,5; 8.0,5; 8.5,2;
9.0,2; 9.5,2; 10.5,1; 14-29: E 0; L: 3.0,2; 3.5,11; 4.0,11; 4.5,12; 5.0,38;
5.5,29; 6.0,15; 6.5,3; 28-43: E 0; L: 2.5,3; 3.0,19; 3.5,30; 4.0,16;
4.5,11; 5.0,25; 5.5,3; 6.0,6; 6.5,3; 7.5,1; 44-62: E 3; L: 2.5,1; 3.0,13;
3.5,11; 4.0,4; 4.5,1; 5.0,1; 65-92: E 18; L: 6.0,1.

2043; 5/2/41; 20h-24h; 32:50, 118:18; C; 0-4: E 90; L: 3.0,1; 5.0,20;
5.5,30; 6.0,32; 6.5,20; 7.0,38; 7.5,43; 8.0,53; 8.5,48; 9.0,33; 9.5,17;
10.0,19; 10.5,6; 11.0,14; 11.5,13; 12.0,7; 12.5,4; 13.0,5; 13.5,3; 14.0,1;
14.5,1; 15.0,2; 7-13: E 16; L: 4.0,1; 4.5,4; 5.0,21; 5.5,19; 6.0,12;
6.5,6; 7.0,10; 7.5,9; 8.0,14; 8.5,15; 9.0,23; 9.5,13; 10.0,26; 10.5,12;
11.0,7; 11.5,11; 12.0,15; 12.5,9; 13.0,7; 13.5,6; 14.0,3; 14.5,3; 15.0,1;
16.0,1; 17-26: E 1; L: 4.5,1; 5.0,2; 5.5,1; 6.0,1; 7.0,1; 9.5,1; 11.5,1;
12.5,1; 13.5,1; 25-33: E 1; L: 4.5,1; 11.5,1; 12.0,1; 14.0,2; 14.5,1;
15.5,1; 30-53: E 0; L: 11.5,1; 52-73: E 0; L: 0; 68-98: E 0; L: 0;
97-142: E 0; L: 0.

2452N; 6/17-18/41; 22h-3h; 32:23, 117:52; C; 0-3: E 1; L: 11.0,1; 12.0,5;
12.5,4; 13.0,3; 13.5,3; 14.0,2; 14.5,1; 15.5,1; 18.5,1; 7-12: E 0; L:
8.5,1; 13.5,1; 14.0,1; 15-24: E 0; L: 9.0,2; 11.0,2; 11.5,1; 12.0,1;
12.5,2; 13.0,1; 13.5,1; 15.0,2; 22-35: E 0; L: 13.0,1; 36-52: E 0; L:
10.5,1; 11.5,1; 14.5,1; 48-84: E 0; L: 0; 57-101: E 0; L: 0; 90-146:
E 0; L: 0.

2452D; 6/18/41; 9h-14h; 32:17, 117:52; C; 0-3: E 0; L: 0; 6-12: E 0;
L: 0; 14-21: E 0; L: 0; 25-36: E 0; L: 11.5,1; 38-43: E 0; L: 11.5,1;
12.5,1; 52-67: E 0; L: 17.5,1; 18.0,1; 68-81: E 0; L: 18.0,1; 96-152:
E 0; L: 0; 125-156: E 0; L: 0.

2454N; 6/18-19/41; 21h-2h; 32:12, 118:38; C; 0-4: E 8; L: 4.5,1; 5.0,2;
6.0,1; 6.5,2; 7.0,1; 9.0,1; 9.5,1; 10.0,1; 10.5,3; 12.5,1; 7-13: E 15;
L: 4.5,1; 5.0,2; 6.0,1; 6.5,2; 8.5,1; 9.0,2; 10.5,1; 11.0,1; 12.0,1;
12.5,1; 18-25: E 1; L: 5.0,1; 7.5,1; 8.0,1; 9.0,3; 9.5,4; 10.0,1; 11.0,2;
12.0,2; 12.5,1; 13.0,1; 13.5,1; 14.0,2; 14.5,2; 15.0,1; 24-32: E 0; L:
4.5,5; 5.0,2; 5.5,1; 7.0,2; 8.5,1; 9.0,2; 9.5,3; 11.0,5; 11.5,3; 12.0,3;
12.5,3; 13.0,4; 17.5,1; 38-52: E 0; L: 10.0,1; 11.0,2; 12.5,1; 52-69:
E 0; L: 0; 66-108: E 0; L: 0; 90-149: E 0; L: 0; 122-208: E 0; L: 0.

2454D; 6/19/41; 8h-13h; 32:10, 118:39; C; 0-3: E 3; L: 6.0,1; 10.0,2;
12.0,1; 12.5,1; 7-14: E 1; L: 0; 17-25: E 0; L: 4.5,1; 6.0,3; 6.5,1;
10.0,1; 23-36: E 0; L: 4.0,2; 4.5,4; 5.5,2; 13.0,1; 36-47: E 0; L:
5.0,1; 12.0,1; 52-69: E 0; L: 21.0,1; 26.0,1; 70-85: E 0; L: 0; 99-121:
E 0; L: 0; 120-198: E 0; L: 0.

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